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RESEARCH ARTICLE

Exotic wild boars and native wild guinea pigs maintain plant diversity in Argentinean coastal grasslands by decreasing plant dominance

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Abstract

Question: In productive grasslands highly dominated by a single plant species, herbivores can promote overall plant diversity. Wild boars (*Sus scrofa*) often decrease species diversity, alter regeneration and change community composition in their native and invader ranges while digging and uprooting vegetation for feeding. In addition, wild guinea pigs (*Cavia aperea*), a small vertebrate herbivore native to South America, concentrate their feeding activities in open patches where they also affect plant diversity, biomass and composition. In this context, can wild-boar disturbances promote plant diversity in herbaceous systems characterized by a highly dominant species? Can native wild guinea pigs magnify these impacts?

Location: Coastal grasslands and salt marshes of the northeastern part of the temperate Argentine pampas, that are dominated by native or exotic herbaceous species.

Methods: We first analyzed alpha- and beta-diversity of plant assemblies in three natural coastal herbaceous areas, invaded by wild boars, through samplings (comparing disturbed and undisturbed areas) and experiments (using exclosures and control plots). Then, we analyzed whether wild guinea pigs could affect patch recovery (alpha- and beta-diversity) after wild-boar disturbances in one site.

Results: Wild boars enhanced alpha-diversity (compared to undisturbed areas) but had no significant effect on beta-diversity. Nevertheless, wild guinea pigs feeding on wild-boar disturbances increased between-patch heterogeneity in species composition (i.e., beta-diversity).

Conclusion: Wild boars remove vegetation in patches that, without subsequent wild-guinea-pig herbivory, dominant species rapidly recover. Wild-guinea-pig herbivory allows different subordinate species to peak at different disturbed patches, contributing to larger species richness at larger scales in areas otherwise occupied by highly dominant plant species. In a wider context, these results imply that the joint action of different-sized exotic and native herbivores can help to maintain plant species diversity in highly plant-dominated grasslands.

KEYWORDS
alpha-diversity, beta-diversity, exotic species, grassland, highly dominated herbaceous systems, salt marsh, wild boar, wild guinea pig

1 | INTRODUCTION

Biological communities are generally dominated by a few species (i.e., a skewed abundance distribution, with a few common species and many rare species; Magurran, 2004). Particularly in productive herbaceous systems, this pattern is driven by competition, where the dominant plant species usually outcompete subordinate species, reducing plant diversity and altering ecosystem functions (Creed et al., 2009). In addition, by altering soil properties, invasive dominant species can cause cascading effects on soil functions, also leading to decreased diversity (Boscutti et al., 2020). However, plant diversity can be increased by large herbivores when they prevent dominance (by targeting dominant species; Koerner et al., 2018; Mortensen et al., 2018), reducing competition intensity by increasing resource availability (e.g., light reaching the understorey; Borer et al., 2014). These effects can be direct (i.e., decreasing dominance consumption), but also mediated by the impact that large herbivores have on smaller-sized herbivores.

In general, large herbivores have negative interactions with smaller-sized vertebrate herbivores as they share the same food resources (Foster et al., 2014). However, large herbivores can also benefit small herbivores, particularly those that prefer short vegetation or more nutrious regrowths (Huisman & Olff, 1998; Van Wieren, 1998; Kuijper et al., 2008; Bakker et al., 2009; Ripple et al., 2015). Until recently, attempts to establish herbivore effects on plant diversity generally took into account herbivore size (as stated above) and provenance (Spear & Chown, 2009), given that shared history over evolutionary times can affect this outcome (Price et al., 2022). Nevertheless, a recent study by Lundgren et al. (2024) showed that the mechanism of herbivore consumption rather than its provenance is a key aspect to understand and predict herbivore's effects on plant diversity, and this may also apply for the outcome of the interactive effect of large and small herbivores.

Wild boars (or feral pig, *Sus scrofa*), introduced from Eurasia, are among the most controversial and widespread consumer species introductions. Wild boars were introduced worldwide by humans, and established on every continent (except in Antarctica), as well as several oceanic islands (Long, 2003). As other generalist exotic consumers, wild boars cause profound community-level impacts (Ricciardi et al., 2013), including local plant extinctions (Risch et al., 2021). Because of their feeding techniques, they often disturb extensive vegetated areas (Baubet et al., 2003; Cushman et al., 2004), generating bare soil patches. In general, these disturbances decrease species diversity, alter regeneration and change community composition (Webber et al., 2010; Boughton & Boughton, 2014). For example, in their native range, wild boars reduce forest tree species richness (Bongi et al., 2017), understorey plant cover and sapling survival (Wirthner et al., 2012), negatively affecting not only plant but also animal diversity within those ecosystems. In addition to those pervasive effects, in their exotic range wild boars can also facilitate the establishment, and increase the biomass, of invasive exotic plants (Cushman et al., 2004; Siemann et al., 2009; Barrios-Garcia & Simberloff, 2013; Nuñez et al., 2013), ultimately affecting multiple components of the ecosystem (Barrios-Garcia & Ballari, 2012). However, disturbances by wild boar do not always increase exotic species richness, as there are some examples of wild boars delaying species invasion (Cuevas et al., 2012). The mechanisms behind the effects of wild-boar disturbance on species richness may depend on the trajectory of the secondary succession (Dovrat et al., 2014) that can be, in turn, mediated by herbivores that ultimately regulate recovery time (Farrell, 1991).

The main herbaceous systems of coastal Buenos Aires (Argentina) are grasslands and salt marshes. On the one hand, salt marshes are strongly dominated by a few native species, mainly the dense-flowered cordgrass, *Spartina densiflora* (Isacch et al., 2006). Coastal grasslands, on the other hand, are being increasingly dominated by several exotic species, particularly, the invasive tall fescue, *Festuca arundinacea*, introduced by humans as a high-quality forage species for livestock (Scheneiter et al., 2016). Given its great accumulation of densely packed above-ground biomass, this grass is replacing native plant species, particularly in abandoned grasslands (i.e., once actively managed for agricultural or other purposes that have been left unattended; Tognetti et al., 2010). Thus, despite being dominated by native or invasive species, plant diversity in both systems may be particularly sensitive to factors that affect, or regulate, their dominance.

Although large native herbivore populations have been decimated (especially over the past 100 years), small vertebrate herbivores (such as wild guinea pigs, *Cavia aperea*), are still highly abundant in Argentinean grasslands and salt marshes (Alberti et al., 2011; Daleo et al., 2014; Pascual et al., 2017). While the impact of large herbivores on plant diversity is more predictable (i.e., they increase diversity in productive sites while they decrease diversity in nutrient-poor sites), small herbivores usually have inconsequential or more idiosyncratic effects (Olff & Ritchie, 1998; Bakker et al., 2006). Nevertheless, the combination of both large and small herbivores generally regulates vegetation more strongly than either alone (Ravolainen et al., 2011; Rebollo et al., 2013; Burkepile et al., 2017). These effects not only occur at the local scale (i.e., patch alpha-diversity), as the combination of differently sized herbivores can strongly homogenize composition at larger spatial scales (i.e., interpatch beta-diversity; Alberti et al., 2017). While wild guinea pigs can locally reduce the biomass of dominant species (Pascual et al., 2019), they concentrate their feeding activities in open patches (i.e., not dominated by tall grasses, either native or exotic; Cassini & Galante, 1992) where they affect plant diversity, biomass and composition (Alberti et al., 2011). Wild guinea pigs can thus regulate the speed of secondary succession after disturbance by suppressing seedlings and limiting clonal colonization of the dominant species (Daleo et al., 2014, 2017).

Grasslands and salt marsh ecosystems along the Argentinean coast are also experiencing the rapid expansion of wild-boar populations (Pérez Carusi et al., 2009). Although their expansion is getting much attention in Argentinean media, there is still comparatively little empirical evidence on their effects (Ballari & Barrios-García, 2022). This threat is expected to increase since it is very likely that they have not reached their maximum potential densities, considering the residence time of wild boar in this ecoregion (10–100 years; Sanguinetti & Pastore, 2016), and the suitability of these habitats for wild boars (La Sala et al., 2023). Wild boars are becoming the most important free-living large consumers in these areas due to the lack of native large herbivores and predators, thus, their impacts on community structure and function are likely increasing. However, there are no studies addressing how exotic wild boars affect diversity at different spatial scales in highly dominated herbaceous systems, and if these effects can be mediated by native small herbivores.

In this context, our first objective is to evaluate whether wild-boar disturbances affect plant diversity in highly dominated herbaceous systems (either by native or exotic species). We hypothesize that in these herbaceous systems, wild boars will increase alpha- and beta-diversity by opening vegetation patches in both grasslands and salt marshes, reducing cover of dominant species, thus favoring subordinated species. Our second objective is to evaluate if those impacts from wild boar could be modulated by wild guinea pigs. We hypothesize that wild guinea pigs will reduce the recovery of dominant species after wild-boar disturbances, ultimately contributing to higher plant diversity.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was carried out in three different natural coastal herbaceous areas (see Appendix S1 for a map and photographs of the study sites), located in the temperate Pampas, Argentina; (i) Canal 1, a Wildlife Refuge (36°19′ S, 57°09′ W), (ii) Campos del Tuyú, a National Park (36°21′ S, 56°51′ W) and (iii) Mar Chiquita, an UNESCO Man and the Biosphere Reserve (37°43′ S, 57°25′ W). The first two sites are located at Bahía Samboromón, in typical high salt marsh communities, with vegetation dominated by two halophytic species, *Spartina densiflora* and *Salicornia neei*, but interspersed in the higher areas with subordinate plants (Isacch et al., 2006; Gonzalez, 2019). These subordinate plants include typical pampas grassland species (such as *Stenotaphrum secundatum*, *Paspalum dilatatum*, *Bromus unioloides*, *Conyza bonariensis*, *Baccharis juncea*, *Acmella decumbens*) and halophytic grasses (such as *Distichlis spicata*, *Paspalum vaginatum*, *Hordeum pusillum*, *Juncus acutus*). The remaining site is located surrounding the Mar Chiquita coastal lagoon, and is a flooded grassland formerly dominated by *S. densiflora*, along with grassland species such as *Bromus catharticus*, *Poa lanigera*, and sparse tussocks of *Cortaderia selloana* with many subordinate species such as *Conyza bonariensis*, *Hydrocotyle bonariensis*, *Briza minor*, *Deyeuxia viridiflavescens*, *Agrostis montevidensis*, *Ambrosia tenuifolia* and *Veronica peregrina*. Over the last ~20 years, this site has been aggressively invaded by *Festuca arundinacea*, an exotic plant species commonly used for pasture (Scheneiter et al., 2016), leading to a taller and more packed vegetation structure. Following *F. arundinacea* expansion, there was a marked decline in plant species richness, a pattern also observed in other Pampas grasslands (Tognetti et al., 2010; Tognetti & Chaneton, 2012; see Appendix S1). Although two of the sites are salt marshes and one is a grassland, all of them are herbaceous systems highly dominated by tall-grass species (native in the salt marshes and exotic in the grassland).

Coastal grasslands and salt marshes of temperate pampas, like many other areas in Argentina, are invaded by wild boars (La Sala et al., 2023). In general, wild boars disturb vegetated areas, uprooting vegetation and turning sediment surface into areas of bare soil (Figure 1). In grasslands, rooting behavior of wild boar increases richness of native and exotic plant species (Cushman et al., 2004); however, exotic species are more able to rapidly colonize and persist in these areas, while native species recover more slowly but steadily (Tierney & Cushman, 2006). In our study sites, the size of disturbed areas can vary, depending in part on soil hardness (more and larger disturbances in wet conditions). Individual disturbance events can range from 0.04 m^2 up to 1 m^2 (with an average of 0.8 m^2; unpubl. data). However, wild boars alone or in groups usually concentrate their feeding activity in a given area, generating large disturbances, as individual uprooted areas accumulate (to more than 100 m^2; see Figure 1).

These systems are also inhabited by other vertebrate herbivores such as very low abundances of the native pampas deer (*Ozotoceros bezoarticus*, a near-threatened species according to IUCN) and the exotic axis deer (*Axis axis*) at the two Samborombón sties. In all three sites, other smaller vertebrate herbivores also occur such as exotic European hares (*Lepus europaeus*) and native wild guinea pigs (*Cavia aperea*), the latter being much more abundant. Particularly, wild guinea pigs concentrate their feeding activities in open patches (i.e, short vegetation patches; Cassini & Galante, 1992). These open patches can be created by a variety of disturbances such as fire, cattle grazing, wrack deposition, biocompaction or vegetation die-off. They can be of variable size but are typically up to 1 m^2, and covered with relatively short vegetation (~50 cm high during the peak of biomass, considerably lower than in dense areas, where vegetation is higher than 100 cm; Pascual et al., 2019). Thus, there is a lack of dominant tall-grass species and a similarity in size between individual wild-boar disturbances and the feeding areas preferred by wild guinea pigs. In this context, it is likely that wild guinea pigs use wild-boar-disturbed areas once the bare area becomes covered by short grasses and forbs.

FIGURE 1 Wild-boar-disturbed areas. (a) Closeup of a recently disturbed small area (~1 m^2). (b) Ground-level view of an intermediate-size disturbed area (~20 m^2). (c) Aerial view of a large area (~100 m^2) heavily disturbed by wild boars. The dotted white line highlights the perimeter of the area uprooted by wild boars.

2.2 | Sampling and experimental design

To quantify if there is an association between disturbance by wild boar and plant diversity (first objective), we performed a field sampling in the two Bahía Samborombón sites, during summer 2022. We randomly selected twelve 36-m^2 plots (i.e., 6-m-sided squares), half of them disturbed (between 40% and 100% of the plot), and the other half undisturbed (no signs of recent disturbance); hereafter named as disturbed and undisturbed plots respectively.

In addition, to experimentally evaluate whether wild boars were indeed leading to the differences found between disturbed and undisturbed plots (see Section 3), we collected data from exclosure experiments initiated during September 2018. These experiments were located at Mar Chiquita and Canal 1 and comprised areas of 6 m × 6 m (initially homogeneous in plant cover and with no signs of recent disturbance by boar) randomly assigned to one of the following two treatments (six replicates each at Mar Chiquita and five replicates each at Canal 1): (1) control, which were unmanipulated areas delimited with wooden stakes in the corners, and (2) wild-boar exclosure, delimited with a metal mesh fence (6 m × 6 m × 0.6 m, 100-cm^2 mesh supported by wooden posts in all corners and at the middle of each side), hereafter named as control and exclosure plots respectively. The mesh of the fence allowed the free movement of all smaller herbivores, including wild guinea pigs. Wild-boar exclosures are widely used to evaluate their impact on other components of the ecosystem (e.g., Barrios-Garcia et al., 2014; Bongi et al., 2017; Cuevas et al., 2020).

Considering the area of our sampling and experimental units, and the typical individual disturbances generated by wild boars (generally <1 m^2, see above), more than one wild-boar-disturbed patch can fit within these plots. In each of the sampling and experimental plots (36 m^2) we estimated alpha- and beta-diversity using presence/absence data (quantifying which plant species occurred in each of those plots; see section 2.3 Statistical analyses). We also determined if plant species found in each plot were native or exotic (see Appendix S2 for a scheme of the sampling and experimental design, and Appendix S3 for a list of the species found).

We also evaluated whether wild guinea pigs could further affect plant composition after wild-boar disturbance (second objective). To address this, we gathered data from another ongoing exclosure experiment located in Mar Chiquita. We performed this experiment only at this site, since wild-boar abundances are lower, hence the chances of wild-boar re-visits to disturbed patches were minimal, otherwise we would not be able to separate the effect of wild guinea pigs from that of wild boars in control plots. In October 2019, fourteen similar areas, recently disturbed by boars (i.e., small individual areas of ~0.23 m^2, with ~0% vegetation cover) were randomly selected and assigned to one of the following two treatments (seven replicates each): (1) control, where small vertebrate herbivores (mainly wild guinea pigs) can move freely, and (2) small vertebrate herbivore exclosures, plastic mesh fences surrounding the wild-boar disturbances (~0.23 m^2; 0.5 m height) and anchored to the ground with metal stakes (1-cm^2 mesh). Although these exclosures could be affecting European hares (*Lepus europaeus*), their densities in this site are extremely low; hares are rarely seen while guinea pigs are much more common. Cover of each plant species in each experimental unit was measured in March 2022 (29 months after the beginning of the experiment). We also measured cover of plant species in one 1-m^2 subplot inside each wild-boar exclosure (36 m^2) described above (for the first objective). Those were used as a reference of an undisturbed condition given that they have not been disturbed for at least four years. Plant cover of all species was visually estimated to the nearest 1% (following the Nutrient Network experimental protocol; Borer et al., 2014). In these three treatments, cover was estimated independently for each species so that total summed cover exceeded 100% for multilayer canopies. The sampling area in the wild-boar exclosures (1 m^2) was greater than in the remaining treatments (~0.23 m^2), increasing the chances of detecting more species. Although it would have been ideal to sample equal areas, this approach turned out to be conservative, given that we consistently found fewer species within exclosures regardless of their larger sampling area (see Appendix S2 for a scheme of the experimental design).

2.3 | Statistical analyses

All the statistical analyses described below were performed per site, and sites were never pooled or compared because we were seeking for generalities and sites had different characteristics. Nevertheless, we also included the effect of site in the following analyses to evaluate if all of them behave in the same way (see Appendix S4). For our first objective, we tested the null hypothesis of no differences in alpha-diversity (i.e., the number of species found per plot) between those disturbed and undisturbed plots or control and exclosures, respectively, using *t*-tests. Given that alpha-diversity at Campos del Tuyú did not meet the homoscedasticity assumption, we log-transformed data. We also evaluated if wild- boar disturbances had a differential effect on native vs exotic plant species using two-way ANOVAs (one per site; considering Disturbance and Provenance as fixed factors). For this analysis, we discarded the species we could not identify. Given that alpha-diversity at Campos del Tuyú did not meet the homoscedasticity assumption, we performed a generalized linear mixed-effect model (GLMM, following Zuur et al., 2009) structuring the variance for the factor Condition (i.e., whether the plot was disturbed or undisturbed; using the "dispformula" function from the *glmmTMB* package for R, Magnusson et al., 2017) instead of a typical two-way ANOVA.

We followed the same approach to test if there were differences in beta-diversity (i.e., variability in species composition between replicates, Whittaker, 1960). In this case, we estimated beta-diversity as the distance of a given plot to its group centroid (Anderson et al., 2011). For that, we first created a dissimilarity matrix per site and design (i.e., sampling or experiment) using the Jaccard index, since we only had presence/absence data (Koleff et al., 2003; the "vegdist" function from the *vegan* package for R, Oksanen et al., 2015), and then we calculated the distance of each plot to its group (i.e., disturbed or undisturbed plots; control or exclosure plots) centroid using the "betadisper" function (*vegan* package, see Appendix S5). We finally evaluated the null hypothesis of no differences between disturbed and undisturbed plots (sampling), or controls and exclosures (experiment), using the homogeneity of multivariate group dispersions test ("permutest" function, *vegan* package; Anderson et al., 2006). Lower beta-diversity indicates a landscape more homogeneous in composition, regardless of the species richness per plot.

Finally, to statistically evaluate our second objective, we performed one-way ANOVAs evaluating the null hypotheses of no differences in alpha-diversity (richness), bare soil, dominant plant species cover (i.e., *Spartina densiflora* or *Festuca arundinacea*) and subordinate plant species cover between the three treatments (control, small vertebrate herbivore exclosure—both in disturbed areas—and wild-boar exclosure). Because subordinate plant species cover (%) did not meet the normality assumption, we transformed data using the square root. For those variables showing significant results, we performed a posteriori Tukey tests to determine which treatments differed from each other. To evaluate the null hypothesis of no differences in beta-diversity, we performed a homogeneity of group dispersion analysis as described above, but in this case, using the Bray–Curtis dissimilarity index, since we had species abundance data for this experiment. All analyses were performed using R (R Core Team, 2024).

3 | RESULTS

Alpha-diversity (i.e., species richness) in 36-m^2 plots was between 50% and 150% higher in disturbed than in undisturbed plots at each study site (Campos del Tuyú: $t=4.10$, $df=10$, $p=0.002$; Canal 1: $t=3.1$, $df=10$, $p=0.01$). Experimental results confirmed this pattern; control plots (disturbed by wild boars) had between 44% and 83% higher plant alpha-diversity than exclosure plots (Canal 1 site: $t=3.73$, $df=8$, $p=0.005$; Mar Chiquita site: $t=3.41$, $df=10$, $p=0.006$; Figure 2). The amount of native vs exotic species was independent of wild-boar disturbance for all sites (i.e., non-significant interaction). We found grater native species richness than exotic, representing the 86% of the total richness identified in sampling sites (i.e., Canal 1 and Campos del Tuyú) and 67% and 80% in experimental sites (i.e., Mar Chiquita and Canal 1). Following the previous results, we also found differences between disturbed and undisturbed plots for the sampling sites and control and exclosures for the experimental sites (see Appendix S6). Finally, we did not find significant effects of wild boars in beta-diversity, neither for the sampling (Campos del Tuyú: $F=1.05$, $df=10$, $p=0.338$; Canal 1: $F=0.97$, $df=10$, $p=0.347$)

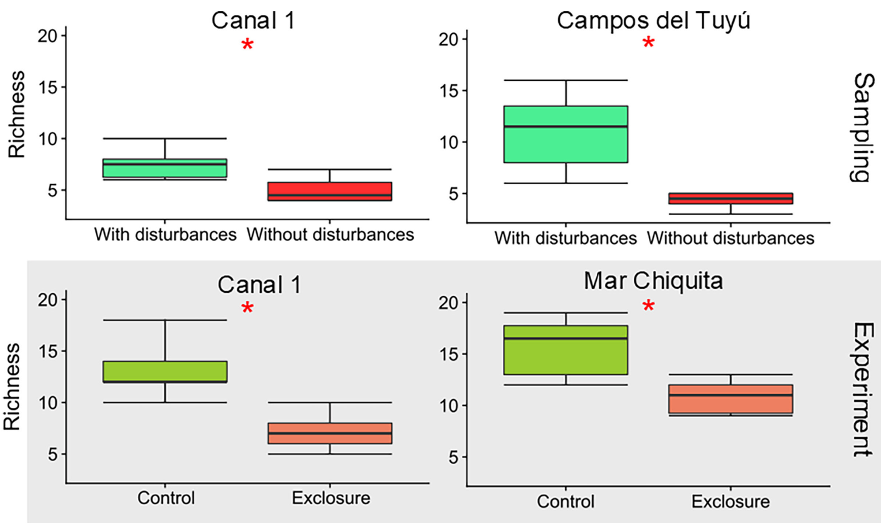

FIGURE 2 Effects of wild boar on plant richness (i.e., alpha-diversity) in 36-m^2 plots from each study site. Here and in the next figures, horizontal bars within box plots represent the median of each treatment, the box represents 50% of the data, and the vertical bars represent the range of the data. Asterisk denotes differences between treatments.

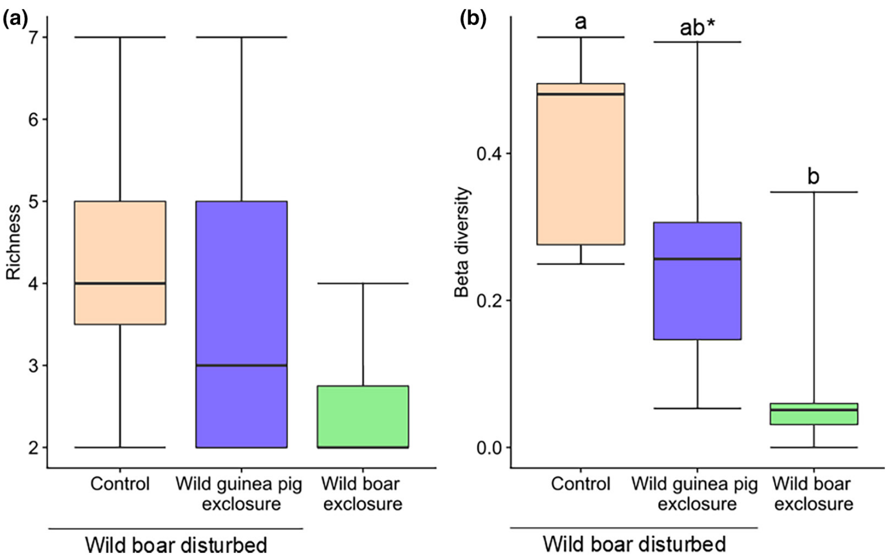

FIGURE 3 Effects of wild guinea pig on (a) richness (i.e., alpha-diversity) and (b) beta-diversity in individual small disturbed areas. Control and wild-guinea-pig exclosure treatments were performed on recently disturbed areas (i.e., bare ground) 29 months before taking measurements. Different letters denote significant differences between treatments. The asterisk next to ab (i.e., ab*) denotes that this treatment was marginally different from the other two treatments (control vs wild-guinea-pig exclosure = 0.082; wild-guinea-pig exclosure vs wild-boar exclosure = 0.077).

nor for the wild-boar exclusion experiment (Canal 1; $F=1.42$, $df=8$, $p=0.292$; Mar Chiquita; $F=1.18$, $df=10$, $p=0.289$).

At the individual wild-boar-disturbed area scale (i.e., ~0.23 m^2), wild guinea pigs did not significantly affect plant alpha-diversity (i.e., species richness; $F=2.13$, $df=2$, 17, $p=0.15$; Figure 3a), but beta-diversity was highest in disturbed plots with wild-guinea-pig herbivory ($F=7.72$, $df=2$, 17, $p=0.004$; Figure 3b). This pattern was similar to the one observed for bare ground which was on average 37% higher in the disturbed plots with wild-guinea-pig herbivory than in the other two treatments ($F=3.61$, $df=2$, 17, $p=0.049$, Figure 4c). Not surprisingly, dominant plant species cover exhibited the opposite pattern ($F=11.48$, $df=2$, 17, $p=0.0007$, Figure 4a), being ~50% lower in the disturbed plots with wild-guinea-pig herbivory than in those excluding guinea pigs. Subordinate species cover was marginally different between disturbed plots and both exclosures (i.e., wild-guinea-pig and wild-boar exclosures), with wild-guinea-pig exclosures showing intermediate values ($F=3.86$, $df=2$, 17, $p=0.09$, Figure 4b).

4 | DISCUSSION

Our field survey and wild-boar exclosure experiments showed that wild boars increased alpha-diversity (plant species richness) in 36 m^2 plots from all study sites (i.e., Campos del Tuyú National Park, Canal 1, and Mar Chiquita), but had no significant effect on beta-diversity (i.e., wild-boar disturbances did not increase landscape heterogeneity in species composition). Nevertheless, wild boars, in combination with wild guinea pigs, indirectly increased beta-diversity in individual small disturbed areas. In other words, wild boars remove vegetation in small individual areas where, without subsequent wild-guinea-pig herbivory, dominant species (i.e., *Festuca arundinacea* and *Spartina densiflora*) eventually reach the cover found in plots undisturbed for (at least) four years (i.e., wild-boar exclosures; see Figure 4a). However, by preventing the expansion of *Spartina densiflora* and *Festuca arundinacea*, wild guinea pigs allow different subordinate species to peak in different small areas (i.e., higher beta-diversity), contributing to higher species richness

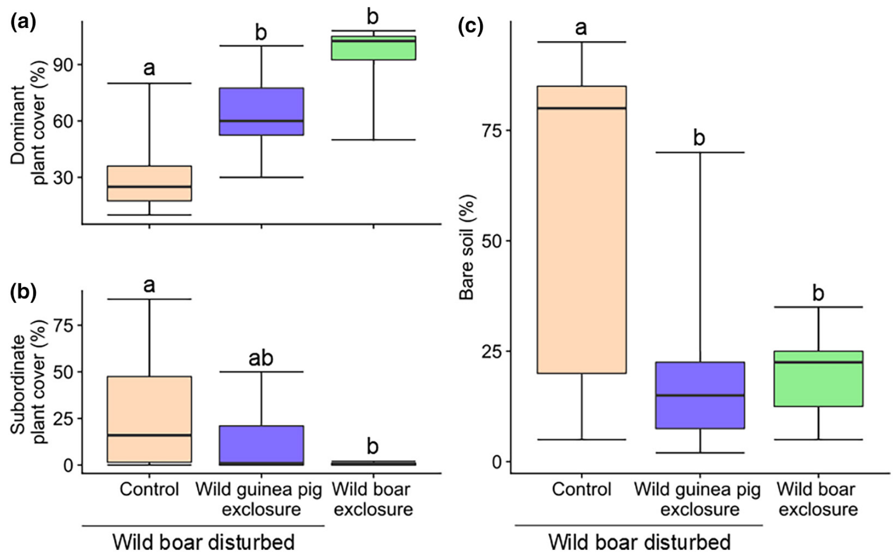

FIGURE 4 Effects of wild guinea pig on (a) plant dominance, (b) subordinate plant species cover and (c) bare soil in individual small disturbed areas. Control and wild-guinea-pig exclosure treatments were performed on recently disturbed areas (with ~0% vegetation cover) 29 months before taking measurements. Different letters denote significant differences between treatments.

at larger spatial scales (i.e., in 36-m^2 plots through different individual small disturbed areas). Overall, this study reveals that wild guinea pigs interact with wild boars to maintain dominant species controlled in otherwise herbaceous systems highly dominated by one species.

4.1 | Exotic large and native small herbivores affect plant diversity at different scales

Wild boars cause major impacts in their native and introduced ranges, especially on community structure and ecosystem function (Barrios-Garcia & Ballari, 2012), although their impacts vary in magnitude and direction. Their most common effect is the decrease of above-ground plant biomass (Barrios-Garcia et al., 2014; Ballari et al., 2020; Gray et al., 2020), with decreases in species diversity (Siemann et al., 2009; Cuevas et al., 2012; Gray et al., 2020) and the alteration of species composition (Siemann et al., 2009; Barrios-Garcia et al., 2014; Bankovich et al., 2016). In some communities, in contrast, rooting by wild boars increases species richness. For example, in a deciduous forest in Sweden, where wild boars are native, they can decrease cover of dominant species, benefiting subordinate poorly competitive species, increasing richness (Wahlgren, 2015). In the long term, they can also increase richness in their exotic range, as has been found in the Argentinean Monte Desert (Cuevas et al., 2020). Nevertheless, and regardless of the direction of their impact, grassland plant communities tend to recover from wild-boar disturbances relatively quickly (native range: Dovrat et al., 2014; introduced range: Baron, 1982; Kotanen, 1995). For the temperate Pampas, however, only a few studies were carried out, mainly regarding population abundances and spatial relationship with native ungulates (see Pérez Carusi et al., 2009, 2017), but none of them addressed community-level impacts. Our results reveal that wild boars increase alpha-diversity (i.e., local plant richness), but have no significant effect on beta-diversity in herbaceous systems with a highly dominant plant species.

The mechanism behind the increase in species richness by boars is likely linked to the effects of herbivores on dominant species. Worldwide, herbivores have differing effects on plant diversity, usually being negative in low-productivity systems and positive in highly productive systems (Osem et al., 2002; Bakker et al., 2006; Hillebrand et al., 2007). In highly productive terrestrial systems only a few tall species tend to dominate and monopolize light, thus reducing this resource to the understorey. If these dominant species are unpalatable, or herbivory-resistant, then herbivores can promote even higher dominance, further reducing light availability for other species, therefore reducing diversity (Koerner et al., 2018). However, if dominant species are palatable, herbivores can reduce their abundance, increasing light availability for subordinate species (Borer et al., 2014), thereby promoting diversity (Koerner et al., 2018). The latter is a likely mechanism in our study region, since wild boars disturb the soil by uprooting plants regardless of whether the species are palatable or not. This reduces dominance, increases resource availability, and thus, promotes diversity. Our study sites are herbaceous systems, characterized by highly dominant species, where subordinate plant species occur in low frequencies or are restricted to rare open areas, unless wild boars (or other disturbances) diminish dominant plant species' above- and below-ground biomass, generating open patches where probably light, space and nutrients are no longer limiting resources. Although we do not know which was the mechanism behind the increased richness in disturbed areas, previous studies in our systems showed that disturbances that remove above-ground vegetation increase both light availability and species richness (Daleo et al., 2017; Pascual et al., 2019). Considering all the preceding information, we suspect that light availability is the most likely mechanism behind increased richness in wild-boar-disturbed areas.

Regardless of the main mechanism regulating the change in species richness, wild boars could be differentially promoting either native or exotic species. With their rooting activity, wild boars can change soil characteristics such as conductivity and nitrogen content, among others (Barrios-Garcia et al., 2014). These abiotic variables can differently modulate richness and abundance of native and exotic plant species (Vitti et al., 2020). Although some studies found that disturbances by wild boars facilitated exotic species (Tierney & Cushman, 2006; Siemann et al., 2009), some others found the opposite pattern (Cuevas et al., 2020; Gray et al., 2020). In our case, we found that wild boars promoted richness of both native and exotic species similarly, natives being the group with more species. Thus, our study sits in the middle between those studies showing that wild-boar disturbances promote exotic over native species and those that show the opposite pattern.

We further showed that wild boars do not regulate richness alone, as small mammal herbivores can magnify the effects of wild boar on plant richness. Large herbivores, by affecting vegetation diversity and biomass, indirectly affect other animals by several mechanisms, such as vegetation consumption, modification of the physical environment, provision and re-distribution of resources (Schmitz, 2008; Marquis, 2010). Small vertebrates can be negatively affected by large native herbivores, since the latter usually reduce biomass and structural complexity of vegetation (i.e., reduction of food resources and/or refuges; Flowerdew & Ellwood, 2001; Foster et al., 2014). Nevertheless, small vertebrates can be benefited by large-herbivore grazing when it generates the re-growth of plants, which usually represent a better nutritional quality than mature leaves (Ydenberg & Prins, 1981; McNaughton, 1984). Hence, large herbivores may reduce food quantity and vegetation height or cover, but improve food quality (Smit et al., 2001) and thus, their impacts may depend on the type of small herbivore.

In the temperate pampas grasslands and salt marshes, the main small herbivore (wild guinea pigs) usually concentrate their feeding activities in areas of short vegetation (Cassini & Galante, 1992). Disturbances by wild boar generate those microhabitats likely benefiting wild guinea pigs. In these areas, wild guinea pigs can maintain the dominant species in low abundances, promoting interpatch heterogeneity in plant composition (i.e., higher beta-diversity between individual small areas). In concordance with our results, a recent study in a highly plant-dominated system also found that herbivore loss can lead to reduced variability in species composition (i.e., low beta-diversity, because the dominant species takes over all areas; Chen et al., 2021). Our results suggest that wild-boar disturbances affect diversity by generating small open areas that are then used by wild guinea pigs as feeding grounds. In each area, wild guinea pigs have a different impact, generating heterogeneity between small areas, thus increasing diversity at larger scales that includes both undisturbed and different disturbed areas.

4.2 | Effects of exotic species belonging to different trophic groups

Exotic species (either plants or animals) are envisioned as having negative effects on communities, particularly when both native and exotic species share a similar trophic group (Vilà et al., 2011; Gallardo et al., 2016; Anton et al., 2019; Xu et al., 2022). Terrestrial exotic primary producers, for example, reduce plant richness, evenness and diversity worldwide (Xu et al., 2022), directly due to evasion of natural enemies, plant adaptation mechanisms, and allelopathy (Davis et al., 2000; Keane & Crawley, 2002), or indirectly, by altering resource availability, such as light and soil nutrients (Boscutti et al., 2020). When exotic and native species do not share the same trophic level, impacts can also be negative (Anton et al., 2019), although lower in magnitude (Vilà et al., 2011). However, some exotic species can benefit others and increase diversity of native species in different systems (Bruschetti et al., 2009; Cuevas et al., 2020; Escapa et al., 2004; Wahlgren, 2015; this study). In the Monte Desert, for example, wild boars promote alpha- and beta-diversity, and this increase is only afforded by native species (Cuevas et al., 2020). In Mar Chiquita, where the rapid expansion of the exotic tall fescue is causing a rapid decline of native plant species, the also exotic wild boars increase plant diversity by disturbing areas monopolized by the tall fescue, reducing competition, and allowing subordinated native species to grow. However, this effect not only takes place in invaded grasslands, given that it also occurs in systems dominated by native plant species (Canal 1 and Campos del Tuyú National Park). Thus, our results emphasize the need to pay attention to the potential undesired effects of the management of wild boars (recently approved in Argentina: RESOL-2021-109-APN-MAD) to control their populations, particularly considering that populations of other free-living native large herbivores are locally extinct or strongly reduced.

The invasion of wild boars in temperate Pampas is relatively recent (~100 years ago; Navas, 1987), and the impacts are thus far relatively moderate compared to what has been demonstrated in other systems (Barrios-Garcia & Ballari, 2012). However, by generating areas of bare soil, wild boars could be opening the door for exotic species to establish (Cushman et al., 2004; Siemann et al., 2009; Barrios-Garcia & Simberloff, 2013; Nuñez et al., 2013). Although further studies should investigate how disturbances by wild boar affect the dynamics of exotic species, our results showed that an exotic species can have positive effects on plant diversity regardless of the plants' provenance, likely mediated by a native small herbivore in grasslands highly dominated by a single plant species. In a broader context, our results suggest that the joint action of differently sized herbivores, native and exotic, can help to preserve plant diversity in highly invaded or dominated grassland systems by a few plant species.

AUTHOR CONTRIBUTIONS

Camila Rocca, Pedro Daleo, Juan Alberti and Oscar Iribarne conceived of the idea and designed methodology; Camila Rocca, Pedro Daleo, Clara Diaz de Astarloa, Jesús Pascual and Juan Alberti collected the data; Camila Rocca, Pedro Daleo and Juan Alberti analyzed the data; Camila Rocca wrote the first draft of this paper; Oscar Iribarne, Juan Alberti and Pedro Daleo revised critically for important intellectual content. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All other authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code for these analyses are available via GitHub (https://github.com/juanalberti/wild_boars).

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SUPPORTING INFORMATION

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

Appendix S1. (A) Location of study sites on the coast of Buenos Aires Province, Argentina. (B) Aerial photographs of the study sites. (C) Ground level photographs of the study sites.

Appendix S2. Scheme of the sampling and experimental design for our two objectives including study sites, number of replicates per site, size of sampling and experimental units, and response variables. Arrows crossing between both objectives indicate that the same exclosure was used for both objectives.

Appendix S3. List of species found in each study site, with their life type and provenance.

Appendix S4. Two-way ANOVA for alpha- and beta-diversity, including Site as a factor.

Appendix S5. Multivariate beta-diversity.

Appendix S6. Two-way ANOVAs for species provenance and disturbance by wildboar.

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