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Original Investigation

Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina

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ABSTRACT

The wild boar (*Sus scrofa*) is an exotic agent of disturbance that arrived in the Ñacuñán Reserve of Argentina in the 1980s. When foraging, the wild boar overturns extensive areas of soil leaving them bare of vegetation. Knowledge is scarce about the boar's impact on vegetation composition and soil properties in the Monte Desert, Argentina. The objective of our study was to determine the short terms effects of wild boar rooting on vegetation and on soil physical, chemical and microbiological properties. Our results indicate that rooting activities significantly reduced the plant cover of herbs, perennial grasses and shrubs, and decreased plant richness and diversity. Disturbed soils showed less compaction, more moisture, a low C/N ratio, and high content of mineral nitrogen. These new soil characteristics could be responsible for a reduced plant cover and less soil bulk density, which could increase soil degradation by wind erosion.

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Introduction

Biotic and abiotic disturbances are widely recognized as key factors influencing the structure and composition of ecosystems (Sousa 1984; Collins and Barber 1985). In terrestrial plant communities, disturbance regimes play an integral role in the spatial and temporal heterogeneity of vegetation (Collins and Barber 1985; Hobbs and Huenneke 1992) and they are an important agent for the maintenance of species diversity (Connell 1978; Huston 1979). But disturbance can also facilitate the introduction and spread of invasive species (Hobbs and Huenneke 1992).

Soil disturbance, especially by animals, often has important effects on the dynamics of the native plant communities (Hobbs and Huenneke 1992). When an organism directly or indirectly controls the availability of resources to other species by its ability to cause physical state changes in biotic and abiotic materials, it is considered an ecosystem engineer (Jones et al. 1994). That is, a species that changes, maintains or creates habitats by modifying the physical state variables of an ecosystem. A wealth of such examples can be found among mammals. For example, invasive beavers (*Castor canadensis*) in Chile reduce riparian forest canopy and tree seedling bank, and increase the abundance and

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richness of the herbaceous cover (Anderson et al. 2006). In the United States of America, the pocket gopher (*Thomomys talpoides*) modifies soil texture, increases the plant-available nitrogen and decreases organic matter (Sherrod and Seastedt 2001), generating a redistribution of soil nutrients. In South Africa, Cape porcupine (*Hystrix africaeaustralis*) modulates the availability of resources to other organisms by favoring more seedlings than in adjacent areas (Bragg et al. 2005). In the United States of America, feral hogs (*Sus scrofa*) modify microhabitat diversity by increasing plant species richness and diversity (Arrington et al. 1999; Tierney and Cushman 2006).

Biological invasions are considered one of the main threats to natural ecosystems (Vitousek et al. 1997). A primary focus of invasion biology is assessing the impact of exotics on native species, communities and ecosystems (Williamson 1996). Invasive species can modify-at the individual level- the rates of survival and reproduction of native species, affecting their population growth. At the community level, they can change its composition and structure; while at the ecosystem level they can modify its structure and function, modifying resource availability and the regime of natural disturbances such as fire cycles (Lockwood et al. 2007). Mack and D'Antonio (1998) recognized two categories of effects of invasive species: (1) species that change physical or biological aspects of the disturbance, and (2) those that change the response of the biota to the disturbance. In addition, invaders themselves can sometimes act as intense agents of disturbance, especially grazing or rooting mammals (Lockwood et al. 2007).

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The wild boar, *Sus scrofa*, was introduced to Argentina in Estancia San Huberto, La Pampa province, in 1906 for hunting purposes (Daciuk 1978). From this colonizing stock, a group was moved to northern Patagonia into Neuquén province. In 1914, some of these animals escaped and colonized several provinces of Argentina (Navas 1987; Novillo and Ojeda 2008). In northern Patagonia, for example, populations of wild boar have increased by nearly 30% during the past 20 years (Pescador et al. 2009). At present, the wild boar occupies many habitats in Argentina from the Patagonian forests and humid pampas to arid and semiarid regions. To obtain their food, wild boars overturn extensive areas of soil, leaving them bare of vegetation. This rooting behavior creates a complex mosaic of disturbed patches of different ages and sizes.

The effect of wild boar as an invasive species and ecosystem engineer is well known around the world, not only from the damage inflicted to agricultural crops (Seward et al. 2004; Wilson 2004), but also from the damage caused to the native biota (Bratton 1975; Singer et al. 1984; Arrington et al. 1999; Tierney and Cushman 2006). Wild boar rooting can affect the composition of plant community by reducing plant cover (Bratton 1974, 1975) and by generating a decreased in richness immediately after boar disturbance (Kotanen 1995; Hone 2002; Cushman et al. 2004). Wild boar generates a decreasing in recruitment rate of holm oak (Quercus ilex) and modifies the spatial distribution of the saplings (Gómez and Hódar 2008). In contrast, Tierney and Cushman (2006) found that rooting activities can benefit in the long term native and exotic floras by increasing their richness and the percent cover of perennial grasses. Wild boar rooting also mixes soil horizons, reduces leaf litter, accelerates the leaching of Ca, P, Zn, Cu and Mg from leaf litter and soil, increases the nitrate concentration in disturbed soils, increases soil respiration, and decreases soil microbial properties and the abundance of saprophageous and predatory soil arthropods (Singer et al. 1984; Mohr et al. 2005; Risch et al. 2010).

In Argentina, studies about the impact of wild boar on vegetation are scarce and there are not studies addressing the impact on soil properties. There are two studies assessing wild boar's impact on plant species. One of them is in northern Patagonia where this species reduces seed survival and seedling regeneration of the conifer *Araucaria araucana* (Sanguinetti and Kitzberger 2010) and the second one is in the Monte Desert biome where wild boar rooting generates a decrease in percentage cover of plant species such as grasses and shrubs (Cuevas et al. 2010).

Wild boars are present in many parts of the Monte Desert biome, but their abundance or density is unknown. This biome has undergone moderate to severe degrees of desertification due to an interaction between the system's own fragility and anthropogenic forces such as cattle grazing, logging, and modification of fire regimes (Villagra et al. 2009). It should be noted that this is one of the Argentinean ecoregions with the highest degree of endemicity of reptiles, mammals, birds and arthropods (Roig et al. 2009). The wild boar was detected in the Monte Desert biome for the first time in the early 1980s. Knowledge about its impact on vegetation composition and soil properties in Monte Desert would be significant for understanding of the wild boar role as a new important factor of disturbance to this biome. The objectives of this study were to assess the short-term impacts of the rooting behavior of wild boars on: (a) plant composition and cover, species richness and diversity, and (b) soil physical, chemical, and microbiological properties.

Material and methods

Study area

The Monte Desert biome of Argentina is dominated by arid and semiarid conditions (Labraga and Villalba 2009). It extends as a

latitudinal wedge across Argentina from the Andean foothills in Salta (24°30'S) to the Atlantic coast in Chubut (44°20'S) (Roig et al. 2009). Our study was conducted in the Man and Biosphere Reserve of Ñacuñán (34°02'S, 67°58'W; 13,200 ha), located in the central region of the Monte Desert. The landscape is characterized by a heterogeneous mosaic of vegetation patches. Dominant habitats are known as "algarrobal" or Prosopis woodland (Prosopis flexuosa), "jarillal" or Larrea shrubland (Larrea cuneifolia), and "medanal" or sand dunes. The vertebrate fauna is diverse. There are few mammal species in the Reserve. Rodents show the highest diversity with 9 species: Akodon molinae, Eligmodontia typus, Calomys musculinus, Graomys griseoflavus, Ctenomys mendocinus, Microcavia australis, Galea musteloides, Dolichotis patagonum and Lagostomus maximus. Carnivores follow in importance with 7 species: Lycalopex griseus, Galictis cuja, Conepatus chinga, Leopardus geoffroyi, Leopardus pajeros, Puma yagouaroundi and Puma concolor. Edentates include several species like Chaetophractus vellerosus, Zaedyus pichiy and the endemic Chlamyphorus truncatus (Rundel et al. 2007). Birds are the most diverse group. There are 82 species being Teledromas fuscus an endemic species (Rundel et al. 2007). Amphibians and reptiles include 4 and 19 species respectively belonging to 10 families: Bufonidae, Leptodactylidae, Cerathophrydae, Testudinidae, Amphisbaenidae, Leurosauridae, Liolaemidae, Gekkonidae, Teiidae, Leptotyphlopidae, Colubridae, Viperidae and Elapidae. The snake Pseudotomodon koslowsky is endemic (Roig et al. 2009). The landforms consist on an undulating to depressed loess-like sandy plain of quaternary fluvial, lacustrine and aeolian origin (Abraham et al. 2009). The climate is semiarid and strongly seasonal, with hot, humid summers and cold, dry winters. Mean annual precipitation is 326 mm. Mean annual temperature is 15.6 °C, with a maximum annual mean of 23.8 °C and a minimum annual mean of 7.6 °C. The wet season goes from November to April and the dry season spans from May to October (Claver and Roig-Juñent 2001; Labraga and Villalba 2009). During the period of study, for the wet season the mean temperature was 20.9 °C and the mean precipitation was 260 mm. For the dry season the mean temperature was 11.3 °C and the mean precipitation was 32 mm.

Field and laboratory analyses

Sampling was conducted twice a year (wet and dry season) during 2008 and 2009. To assess the impact of wild boar rooting on vegetation and soil properties, we set up transects along the whole length of the inner and perimeter trails of the reserve in search of feces and signs of wild boars rooting (Cuevas et al. 2010). The total length of the transects was 75.01 km (Fig. 1). We recorded every rooting activity within 10 m on either side of each transect. The distance between selected sites was 250 m in order to minimize data-dependence (Abaigar et al. 1994). At each selected sites, a disturbed patch was paired with an undisturbed patch for observation, in which we randomly distributed 10 plots ($60 \text{ cm} \times 60 \text{ cm}$) within each patch type. At each plot we measured the percentage cover of plant species and litter by visual assessment, and estimated species richness and diversity by calculating the Shannon Weaver diversity index (Zar 1999). Rooting entails breaking through the surface layer of vegetation, followed by excavation to a depth typically ranging between 5 and 15 cm (Kotanen 1995). In the study area the mean extension of the rooting patches were 46.3 m².

Undisturbed patches were established adjacent to the disturbed ones to guarantee that the former represented a similar habitat as the latter before being rooting by wild boars (Cuevas et al. 2010). For field analysis we only considered recent rooting within each season. This means the age of rooting ranged from 0 to 4 month old. Recent damage was identified by a loose soil surface and a scarcity of colonizing plants. From one season to the next one, the rooting sites were not the same.

M.F. Cuevas et al. / Mammalian Biology 77 (2012) 299-306

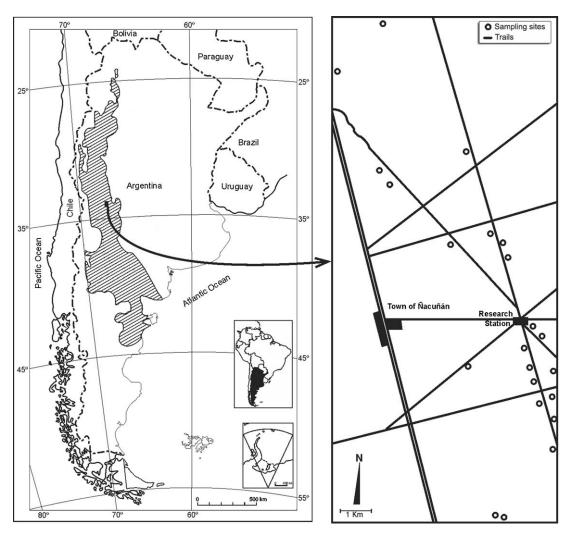


Fig. 1. Location of the Reserve of Ñacuñan, showing the inner and perimeter trails and the location of the sampling sites.

To study the impact on soil physical and chemical properties we measured at each site the following attributes: soil hardness (in the field) with a penetrometer at three different depths (5, 10 and 15 cm depth; Herrick et al. 2005), soil moisture by gravimetry, texture by Bouyoucos method (Klute 1986), total organic matter content (TOM) by the wet-digestion method of Walkley and Black (Nelson and Sommers 1982), total nitrogen content (TN) by Kjeldahl method (Keeney and Nelson 1982), mineral nitrogen content (ammonium and nitrate + nitrite) by micro Kjeldahl analysis (Keeney and Nelson 1982), pH, organic carbon, and carbon/nitrogen ratio.

Regarding microbiological attributes, under standardized soil conditions in the laboratory ($28-30 \circ C - 60\%$ water-holding capacity) we analyzed total heterotrophic activity through soil respiration by the CO₂ release method (during seven days; Alef 1995). Abundance of different functional groups of microorganisms was quantified by the most probable number (MPN) for ammonifier, nitrifier and cellulolytic organisms, and direct cell counts by agar plate methods for nitrogen-fixing organisms (Döbereiner 1995; Lorch et al. 1995). Samples were incubated at $28 \circ C$ for 5–21 days depending on the functional group.

Soil hardness data were collected from 10 points (subsamples) in disturbed patches and 10 points in undisturbed patches. We used a modified penetrometer (Herrick et al. 2005) consisting of a 1-m scaled stick and a 500 g weight. At each point we recorded the number of strokes necessary to penetrate into three soil depth levels:

5 cm, 10 cm and 15 cm. For the remaining attributes, we took 20 subsamples of soil (10 from disturbed and 10 from undisturbed patches). We pooled the subsamples and took two samples per site (one from a disturbed and one from an undisturbed patch) for subsequent laboratory analysis. Chemical and microbiological properties were analyzed only during the second year (2009).

Statistical analyses

To compare compositional plant identity between disturbed and undisturbed patches, we conducted a principal components analysis (PCA) using percentage plant species cover. To detect differences in vegetation richness, diversity and plant species cover between disturbed and undisturbed patches, we carried out a Wilcoxon paired test, also used for the characterization of the differences among soil physical and chemical properties between patches. To detect responses of microbiological attributes at disturbed and undisturbed patches we used a paired t test. We applied a transformation to those data not meeting the assumptions of normality. Data on percentages were arcsine square-root transformed, and data on abundance of microorganisms were log transformed prior to analysis (all above procedures according to Zar 1999). We performed all statistical analyses with InfoStat 2009 version (Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina).

302

M.F. Cuevas et al. / Mammalian Biology 77 (2012) 299-306

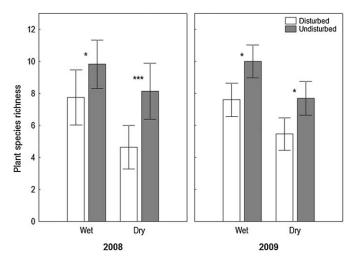


Fig. 2. Plant species richness (mean ± 2 SE) in undisturbed patches (UP, filled bars) and in those disturbed by wild boars (DP, open bars) during two years of study.

Results

Vegetation disturbance by rooting behavior

As Table 1 shows, in the first year of the study (2008) and during the wet season (n = 12) we found significant differences in plant cover of eight species (out of 37) between disturbed and undisturbed patches. During the dry season (n = 14) we found that only ten plant species (out of 29) showed significant differences between patches. In the second year of our study (2009), during the wet season (n = 10) we found significant differences in plant cover for only eight species (of a total of 29 species), and during the dry season (n = 13) only six species out of 21 showed significant differences between disturbed and undisturbed patches.

In both seasons over the two years of study, plant richness (Wilcoxon paired test, wet season 2008: n = 12; T = 12, Z = 2.12, p = 0.03; dry season 2008: n = 14; T = 0, Z = 3.06, p = 0.002; wet season 2009: n = 10; T = 1, Z = 2.70, p = 0.007; dry season 2009: n = 13; T = 7, Z = 2.51, p = 0.012) and diversity index (Wilcoxon paired test, wet season 2008: n = 12; T = 4, Z = 2.74, p = 0.006; dry season 2008: n = 14; T = 10, Z = 2.67, p = 0.007; wet season 2009: n = 10; T = 8, Z = 2.00, p = 0.046; dry season 2009: n = 13; T = 9, Z = 2.55, p = 0.011) were significantly higher in undisturbed patches (Figs. 2 and 3). The

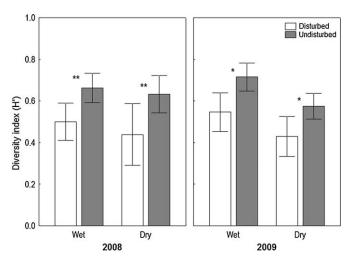


Fig. 3. Plant diversity index (H') (mean ± 2 SE) in undisturbed patches (filled bars) and those disturbed by wild boars (open bars) during two years of study **P*<0.05, ***P*<0.01.

	Species	2008				2009			
		Wet season		Dry season		Wet season		Dry season	
		Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed
	Baccharis angulata			0.01 (0.01)	0.62 (0.28)	1.06 (0.63)	2.37 (0.91)		
	Conyza sp	0.10(0.07)	0.52(0.26)						
	Glandularia mendocina	1.15(0.39)	6.88 (1.17)	0.78(0.33)	1.26(0.33)	0.02 (0.01)	0.16(0.13)		
Herbs	Heliotropium mendocinum	0.03(0.03)	0.37 (0.22)						
	Sphaeralcea miniata	0.33(0.21)	1.98(0.81)						
	Pitraea cuneato-ovata	15.06 (2.95)	2.92 (0.75)						
	Plantago patagonica			0	0.12(0.05)				
	Digitaria californica			0.01(0.01)	0.49(0.38)	0.17 (0.10)	0.58(0.26)	0.11(0.10)	(0.01)
	Pappophorum sp			0.46(0.17)	8.58 (2.44)	0.80 (0.31)	6.48(1.56)	0.31(0.13)	4.96 (1.13)
(Setaria sp			0.15(0.11)	0.37 (0.20)	0.33 (0.19)	1.09(0.4)		
Lasses	Sporobolum criptandrus					0.01 (0.01)	2.37(0.91)	0.06(0.05)	0.65 (0.25)
	Stipa sp	1.43(0.68)	4.93 (1.97)	0.53(0.16)	7.86(1.92)		7,46(2,37)	0.45(0.28)	7.12 (2.15)
	Trichloris crinita	0	0.14(0.09)	0.17(0.14)	0.50(0.23)			0.02(0.02)	0.77 (0.53)
	Acantholippia seriphioides							0.04(0.04)	0.25 (0.17)
Shrubs	Larrea cuneifolia			1.84(0.73)	3.41(0.91)				
	Lycium sp	0.21(0.21)	1.46(0.76)	0.06(0.03)	2.76(1.33)	0.08 (0.06)	2.70 (0.99)		
Litter				7.84(1.23)	32.57 (4.68)	9.55 (1.18)	33.18 (4.41)	8.79 (1.76)	32.82 (3.70)

cover percentages of all plant species were also significantly higher in undisturbed patches, except for the annual herb Pitraea cuneatoovata, which presented higher plant cover in disturbed patches (Table 1). Most of the species affected by rooting activity were herbs and perennial grasses. The percentage of cover of the shrub Lycium sp. was significantly lower in the rooting patches during the whole study period. Litter was significantly lower in disturbed patches in three out of four field seasons. The main difference between wet and dry seasons and the two years was the identity of plant species affected by rooting behavior (Table 1).

The PCA of plant species composition extracted two components accounting for 100% of variation (Fig. 4). PC1 was positively associated with Stipa sp, Baccharis angulata, Digitaria californica, Setaria sp, Trichloris crinita, Conyza sp, Pappophorum sp, Sporobolum criptandrus, Lycium sp, Glandularia mendocina, Heliotropium mendocinum and Acantholippia seriphioides. PC2 was positively associated with Pitraea cuneato-ovata, and negatively associated with Sphaeralcea miniata, Larrea cuneifolia and Plantago patagonica. This analysis showed that disturbed patches were associated with presence of *P. cuneato-ovata*, the only species that presented higher percent cover in such patches. PC1 represents 77.9% of the total variation and apparently is the main factor that determines the clustering observed.

Disturbance of soil properties

Physical properties

During the wet season (n = 14) of 2008, patches disturbed by wild boar showed lower soil hardness at all three different depths (p < 0.001 for the three depths; 5 cm: T = 766, Z = 3.21; 10 cm: T=443, Z=6.46; 15 cm: T=647, Z=6.06) and higher soil moisture (T=8, Z=2.62, p<0.01). During the dry season (n=15), only soil hardness showed significant differences between soils at the three different depths, with disturbed patches being less compacted than undisturbed ones (p < 0.001 for all three depths; 5 cm: *T* = 128, *Z* = 8.24; 10 cm: *T* = 1051, *Z* = 7.45; 15 cm: *T* = 1720, *Z* = 6.30). Soil moisture showed no significant differences between patches (T=62, Z=0.31, p=0.76) (Table 2).

In the second year (2009), we found significant differences during the wet season (n = 15) among all three depths between patches, with disturbed patches (D) being less compacted than undisturbed (UD) ones (*p* < 0.001 for the three depths; 5 cm: *T* = 854.5, *Z* = 2.87; 10 cm: T=1983, Z=5.80; 15 cm: T=2822, Z=3.88). Soil moisture was significantly higher in disturbed patches (T=21, Z=2.22, p = 0.02). In relation to texture, the percentage of silt and clay was higher in undisturbed patches (mean D = 11.8, mean UD = 14, T = 7.5, Z = 2.65, p = 0.01 and mean D = 19.0, mean UD = 22.5, T = 7.5, Z=2.65, p=0.008, respectively), while the percentage of sand was higher in disturbed patches (mean D = 69.2, mean UD = 63.4, T = 7.5, Z=2.65, p=0.002) (Table 2). During the dry season (n=13), soil compaction was significantly lower at all depths (p < 0.001 for the three depths; 5 cm: *T* = 203, *Z* = 6.80; 10 cm: *T* = 693, *Z* = 7.31; 15 cm: T = 1792.5, Z = 5.10) in disturbed patches, whereas soil moisture was not significantly different between patches (T = 29, Z = 0.78, p = 0.29)(Table 2).

Chemical properties

In the wet season the C/N ratio was higher in disturbed patches (mean D = 11.1, mean UD = 9.6, T = 26, Z = 1.93, p = 0.042; Table 3). During the dry season (n = 13) only the nitrates + nitrites of the mineral nitrogen and C/N ratio were significantly higher in disturbed patches (mean *D*=16.3, mean UD=6.7, *T*=0, *Z*=3.18, *p*<0.0001 and mean D=9.7, mean UD=9.0, T=14, Z=2.20, p=0.02 respectively). No significant differences between patches were found for the remaining chemical attributes (Table 3).

Physical soil properties		2008						2009					
		Wet season			Dry season			Wet season			Dry season		
		Disturbed	Undisturbed	р	Disturbed	Undisturbed	d	Disturbed	Undisturbed	р	Disturbed	Undisturbed	d
Hardness (no. strokes)	5 cm	2.42 (0.17)	2.82 (0.14)	0.0001*	0.94(0.07)	1.99(0.09)	<0.0001*	2.01 (0.10)	2.39 (0.08)	<0.0001*	1.23 (0.05)	2.04 (0.11)	<0.0001*
	10 cm	5.86(0.43)	9.61(0.50)	<0.0001*	3.84(0.31)	7.09(0.34)	<0.0001*	5.30(0.29)	8.15 (0.34)	<0.0001*	3.65 (0.22)	6.56(0.43)	<0.0001*
	15 cm	10.87(0.70)	18.46(1.12)	<0.0001*	9.92(0.69)	15.52(0.76)	<0.0001*	10.69(0.52)	16.02 (0.73)	<0.0001*	8.90 (0.64)	12.70 (0.43)	<0.0001*
Moisture (%)	10.72 (1.20)	7.54(0.67)	<0.01*		10.04(0.61)	9.66(1.09)	0.75	4.03(0.43)	3.48 (0.40)	0.008*	4.38 (1.04)	4.20(0.78)	0.40
E	Silt							19.04(1.34)	22.53 (1.27)	0.0036*	21.08 (1.32)	22.08 (1.79)	0.53
lexture	Clay							11.75(0.86)	14.00(0.82)	0.006*	13.15(0.88)	13.77 (1.17)	0.65
(Z^Z)	Sand							69.17 (2.20)	63.42 (2.09)	0.004*	64.23 (2.95)	65.77 (2.19)	0.30

Mean (SE) of physical soil properties in disturbed and undisturbed patches between wet and dry seasons during 2008 and 2009.

Table 2

Significant differences existed between disturbed and undisturbed patches

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M.F. Cuevas et al. / Mammalian Biology 77 (2012) 299-306

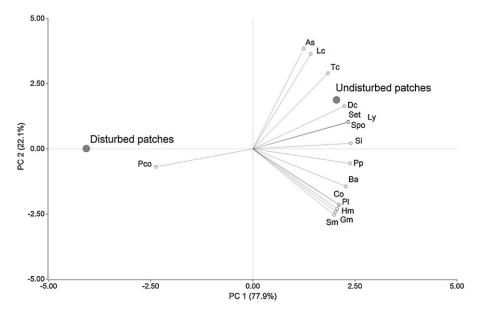


Fig. 4. Principal Component Analysis shows compositional plant identities between undisturbed patches and those disturbed by wild boars. As = Acantholippia seriphioides, Lc = Larrea cuneifolia, Tc = Trichloris crinita, Dc = Digitaria californica, Set = Setaria sp, Ly = Lycium sp, Spo = Sporobolum cryptandrus, Si = Stipa sp, Pp = Pappophorum sp, Ba = Baccharis angulata, Co = Conyza sp, Pl = Plantago patagonica, Hm = Heliotropium mendocinus, Gm = Glandularia mendocina, Sm = Sphaeralcea miniata, Pco = Pitraea cuneato-ovata.

Microbiological properties

The microbial activity measured as soil respiration was higher in undisturbed patches during the wet season (mean D = 0.25, mean UD = 0.31, t test: n = 10, t = -2.28, df = 9, p = 0.048; Table 3). The remaining microbiological attributes did not show any significant differences between patches.

Discussion

Our results support the hypothesis that the overturning of soil by wild boars has an important impact on the composition and cover of vegetation, as well as on some physical, chemical and microbiological attributes of soil in the Monte Desert biome. Undisturbed patches systematically presented a higher cover of plant species, which suggests that rooting activity has a negative effect on the cover of perennial grasses, shrubs and annual herbs. Only the annual herb *Pitraea cuneato-ovata* cover was higher in disturbed patches during the wet season, as previously reported by Cuevas et al. (2010), benefiting from wild boar disturbance. A reason could be that *P. cuneato-ovata* is a highly water-demanding plant, growing in shallow swampy areas where it forms colonies (Stasi and Medero, 1983). The success of this species in disturbed patches could be due to the soil physical properties modified by wild boars, such as decreased soil hardness and increased moisture during the wet season. This did not occur during the dry season, where soil moisture did not differ between patches.

Previous works have shown that the main plant groups affected by rooting behavior are annual and perennial forbs and grasses (Bratton 1974, 1975; Campbell and Rudge 1984; Cushman et al. 2004). We found six species of grasses (*Digitaria californica, Pappophorum* sp., *Stipa* sp., *Setaria* sp., *Trichloris crinita* and *Sporobolum criptandrus*), six species of annual herbs (*Baccharis angulata, Conyza* sp., *Glandularia mendocina, Heliotropium mendocinum, Sphaeralcea miniata* and *Plantago patagonica*), and three species of shrubs (*Acantolippia seriphioides, Larrea cuneifolia* and *Lycium* sp.) that were negatively affected by rooting behavior; and thus were responsible for the decreased richness and diversity immediately after wild boar disturbance that we found. All these plant species are native. We did not find any exotic plant species in none of the sites of this

Table 3

Mean (SE) chemical and microbiological soil properties in disturbed and undisturbed patches between wet and dry seasons during 2009. An asterisk indicates that significant differences existed between disturbed and undisturbed patches.

Soil properties		2009					
		Wet season			Dry season		
		Disturbed	Undisturbed	р	Disturbed	Undisturbed	р
	Total nitrogen (mg kg ⁻¹)	742.93 (34.03)	850.27 (53.26)	0.23	725.85 (98.25)	686.00 (68.27)	0.98
	Mineral nitrogen (mg kg ⁻¹)	32.86 (1.90)	28.70 (2.47)	0.18	25.17 (3.56)	13.95 (1.87)	0.0016^{*}
	Nitrate + nitrite (mg kg ⁻¹)	16.13 (1.29)	13.65 (1.33)	0.32	16.32 (3.37)	6.70 (1.09)	<0.0001*
	NH_4 (mg kg ⁻¹)	16.73 (1.02)	15.05 (1.27)	0.26	8.86 (1.40)	7.24 (1.13)	0.27
Chemical	Organic carbon (%)	0.82 (0.04)	0.82 (0.06)	> 0.99	0.66 (0.07)	0.66 (0.09)	0.95
	C/N ratio	11.10 (0.43)	9.64 (0.35)	0.042^{*}	9.66 (0.27)	8.96 (0.20)	0.029^{*}
	Organic matter	1.41 (0.07)	1.41 (0.10)	> 0.99	1.14 (0.11)	1.13 (0.16)	>0.99
	pH	7.97 (0.03)	7.99 (0.04)	0.54	7.93 (0.03)	7.94 (0.02)	0.79
Microbiological	Soil respiration (mg CO ₂ 7 d ⁻¹ g ⁻¹)	0.25 (0.02)	0.31 (0.03)	0.048^{*}	0.11 (0.02)	0.16 (0.04)	0.33
	Ammonifiers (log g^{-1})	7.91 (0.63)	8.23 (0.49)	0.72	7.37 (0.33)	6.97 (0.10)	0.23
	Cellulolytics $(\log g^{-1})$	6.17 (0.33)	6.52 (0.43)	0.48	7.68 (0.90)	7.40 (0.94)	0.78
0	N fixers $(\log g^{-1})$	6.93 (0.12)	7.10 (0.06)	0.12	6.45 (0.18)	6.32 (0.11)	0.56
	Nitrifiers $(\log g^{-1})$	2.19 (0.37)	1.71 (0.47)	0.50	0.81 (0.41)	0.75 (0.38)	0.91

* Significant differences existed between disturbed and undisturbed patches

study. The only exotic species present in the study area is Salsola *kali* but it is restricted in areas where we did not find any rooting activity. Kotanen (1995) and Cushman et al. (2004) also found that richness and diversity index decreased immediately after disturbance, but a few years later (10 years) both components increased in disturbed soils. In the case of the species richness of native plants increased slowly but steadily through time, whereas richness of exotic species rebounded much more rapidly (Tierney and Cushman 2006). On the contrary, Arrington et al. (1999) found an increase of plant species richness and diversity ten months after rooting. In this study we only measured the short-term impacts of wild boar. Even though the interaction between soil disturbances and sources of propagules play an important role in controlling early stages of succession in newly created gaps (Kotanen 1996), we suggest that the negative effect on plant cover can be explained by the foraging activity of wild boars, because several species such as P. cuneato-ovata, Sphaeralcea miniata, Conyza sp., Plantago patagonica, Pappophorum sp., Stipa sp. and Lycium sp. are included in their diet (Cuevas et al. 2010), and/or because the mechanical force exerted by wild boars that leaves the plant roots exposed as we could observe at field.

In relation to soil physical attributes, the higher moisture content in disturbed soils can be explained because the capillarity is broken, and therefore evaporation is lower. This effect may be related to aeration of the topsoil by wild boar rooting (Moody and Jones 2000). The lower amount of clay and silt in disturbed soils could be explained by the removal of these particles by the wind, as they are broken down by the action of the wild boar. This could also be explained by the mixture of soil horizons resulting from wild boar disturbance, as found by Singer et al. (1984) and Mohr et al. (2005). However, soil texture is a conservative soil property, which is important for plant growth, and is less sensitive to environmental change over short periods of time (Moody and Jones 2000).

On the other hand, in arid environments, soil fertility is the result of seasonal and inter-annual climate variability (Austin et al. 2004). Soil nitrogen availability depends on mineralization of organic matter and microbial activity, which are primarily controlled by precipitation inputs (Carrera et al. 2009). The mineralization rate can be modified due to temperature, soil moisture, and oxygenation. The higher C/N ratio found in disturbed patches indicates that nitrogen mineralization was faster in these soils than in undisturbed ones. This may be accounted for by the increased soil moisture and oxygenation (lower soil hardness) in these areas or by the incorporation of litter into the soil, which was clearly reduced in disturbed patches. We also found a higher content of mineral nitrogen as nitrates and nitrites in disturbed patches. This is consistent with the high mineralization rate found in these soils. The longer the times span between the processes of mineralization and the requirements of the new vegetation, the lower the efficiency of nutrient uptake and use. When mineral nitrogen is released during periods without vegetation, it is subjected to loss by leaching or volatilization (Abril 2002). Thus, the high contents of mineral nitrogen found in disturbed soils could be lost due to rains, leaving the soil without the nitrogen necessary for future plant growth. Our results support the observations of Singer et al. (1984) but differ from those of Cushman et al. (2004) in that the latter did not find any difference in mineralization rate between disturbed and undisturbed patches. Contrary to the results of Risch et al. (2010), we found that soil respiration presented lower values in disturbed patches.

In summary, our study shows that the short-term effects of wild boar rooting are to decrease plant cover and modify plant species composition in the Monte Desert. Although the impact of wild boars is a microsite level, the physical degradation of soil by rooting has consequences on its chemical properties. These new soil characteristics plus the direct impact of wild boars could be responsible for a reduced plant cover and less soil bulk density, which could increase soil degradation by wind erosion. Even though this impact is at microsite scale, disturbance by wild boars could be another factor contributing to accelerate the desertification process in the Monte Desert.

Although the amount of damage produced by wild boar is influenced by their local density (Hone 2002), neither in Argentina nor in the Reserve there is no information on population parameters of this species. We believe that future studies may clarify this.

In the context of regional climate change, the central region of the Monte is experiencing an increase in precipitation and temperature (Labraga and Villalba 2009). If this process continues, we could expect an increase in the rate of lixiviation of nitrogen because of wild boar rooting activities. Additionally, these disturbed patches could become more homogeneous, because the only species that is benefited is *P. cuneato-ovata*, due to its high water-demanding characteristics.

It would be interesting not only to carry out long-term studies and thus ascertain whether the effects of rooting activities remain over time, but also to increase the scale of the study area for a better understanding of wild boar impact on Monte Desert biome. Because impacts by invasive species are so varied and influenced by a broad range of factors (Williamson 1996), it is important to formulate studies that will aid us to understand how these species interact with the new environment. These will provide stronger scientific basis in the design of management strategies for invasive species and invaded ecosystems.

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References

- Abaigar, T., del Barro, G., Vericad, J.R., 1994. Habitat preference of wild boar (Sus scrofa L., 1758) in a Mediterranean environment. Indirect evaluation by signs. Mammalia 58, 201–210.
- Abraham, E.M., del Valle, H.F., Roig, F., Torres, L., Ares, J.O., Coronato, F., Godagnone, R., 2009. Overview of the geography of the Monte Desert biome (Argentina). J. Arid Environ. 73, 144–153.
- Abril, A., 2002. La microbiología del suelo: su relación con la agricultura sustentable. In: Sarandón, S.J. (Ed.), Agroecología. El camino hacia una agricultura sustentable. Ediciones Científicas Americanas, La Plata, Argentina, pp. 129–150.
- Alef, K., 1995. Soil respiration. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, United Kingdom, pp. 214–219.
- Anderson, C.B., Griffith, C.R., Rosemond, A.D., Rozzi, R., Dollenz, O., 2006. The effect of invasive North American beavers on riparian plant communities in Cape Horn Chile. Do exotic beavers engineer differently in sub-Antarctic ecosystems? Biol. Conserv. 128, 467–474.
- Arrington, D.A., Toth, L.A., Koebel Jr., J.W., 1999. Effects of rooting by feral hogs Sus scrofa L. on the structure of a floodplain vegetation assemblage. Wetlands 9, 535–544.
- Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235.
- Bragg, C.J., Donaldson, J.D., Ryan, P.G., 2005. Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. J. Arid Environ. 61, 261–275.
- Bratton, S.P., 1974. The effect of the European wild boar (Sus scrofa) on the highelevation vernal flora in Great Smoky Mountains National Park. Bull. Torrey Bot. Club 101, 198–206.
- Bratton, S.P., 1975. The effect of the European wild boar *Sus scrofa*, on gray beech forest in the Great Smoky Mountains. Ecology 56, 1356–1366.

M.F. Cuevas et al. / Mammalian Biology 77 (2012) 299-306

- Campbell, D.J., Rudge, M.R., 1984. Vegetation changes induced over ten years by goats and pigs at Port Ross Auckland Islands (SubAntarctic). N.Z. J. Ecol. 7, 103–118.
- Carrera, A., Mazzarino, M., Bertiller, M., del Valle, H., Carretero, E., 2009. Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina. J. Arid Environ. 73, 192–201.
- Claver, S., Roig-Juñent, S., 2001. El desierto del Monte: La Reserva de Biosfera de Ñacuñán. IADIZA, MAB, UNESCO, Triunfar, Argentina.
- Collins, S.L., Barber, S.C., 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64, 87–94.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
- Cuevas, M.F., Novillo, A., Campos, C., Dacar, M.A., Ojeda, R.A., 2010. Food habits and impact of rooting behaviour of the invasive wild boar, *Sus scrofa*, in a protected area of the Monte Desert, Argentina. J. Arid Environ. 74, 1582–1585.
- Cushman, J.H., Tierney, T.A., Hinds, J.M., 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. Ecol. Appl. 14, 1746–1756.
- Daciuk, J., 1978. Estado actual de las especies de mamíferos introducidos en la Subregión Araucana (Rep Argentina) y grado de coacción ejercido en algunos ecosistemas surcordilleranos. Anales de Parques Nacionales 14, 105–130.
- Döbereiner, J., 1995. Isolation and identification of aerobic nitrogen fixing bacteria from soil and plants. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, United Kingdom, pp. 134-141.
- Gómez, J.M., Hódar, J.A., 2008. Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). For. Ecol. Manag. 256, 1384–1389.
- Herrick, J.E., Van Zee, J.W., Havstad, K.M., Burkett, L.M., Whitford, W.G., 2005. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems Volume II: Design, Supplementary Methods, and Interpretation. University of Arizona Press, Tucson, Arizona.
- Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6, 324–337.
- Hone, J., 2002. Feral pigs in Namadgi National Park Australia: dynamics, impacts and management. Biol. Conserv. 105, 231–242.
- Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101. Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos
- 69, 373–386. Keeney, D., Nelson, D., 1982. Nitrogen inorganic forms. In: Page, A.L., Miller, R., Keeney, D. (Eds.), Methods of Soil Analysis. Chemical and Microbiological Properties, vol. 2. American Society of Agronomy and Soil Science, Madison, WI, pp.
- 643–698. Klute, A., 1986. Methods of Soil Analysis. Physical and Mineralogical Methods, vol. 1. American Society of Agronomy and Soil Science, Madison, WI, 980 pp.
- Kotanen, P., 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. Ecography 18, 190–199.
- Kotanen, P., 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. Oecologia 108, 652–662.
- Labraga, J., Villalba, R., 2009. Climate in the Monte Desert: past trends, present conditions, and future projections. J. Arid Environ. 73, 154–163.
- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2007. Invasion Ecology. Blackwell Publishing, Oxford, United Kingdom.
- Lorch, H.J., Benckieser, G., Ottow, J.C.G., 1995. Basic methods for counting microorganisms in soil and water. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, United Kingdom, pp. 146–161.
- Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13, 68–75.

- Mohr, D., Cohnstaedt, L.W., Topp, W., 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. Soil Biol. Biochem. 37, 693–700.
- Moody, A., Jones, J.A., 2000. Soil response to canopy position and feral pig disturbance beneath Quercus agrifolia on Santa Cruz Island California. Appl. Soil Ecol. 14, 269–281.
- Navas, J.A., 1987. Los vertebrados exóticos introducidos en la Argentina. Revista del Museo Argentino de Ciencias Naturales. Serie Zoología XIV, 7–38.
- Nelson, D.W., Sommers, L.E., 1982. Total carbon organic carbon and organic matter. In: Page, A.L., Miller, R., Keeney, D. (Eds.), Methods of Soil Analysis. Chemical and Microbiological Properties, vol. 2. American Society of Agronomy and Soil Science, Madison, WI, pp. 539–580.
- Novillo, A., Ojeda, R.A., 2008. The exotic mammals of Argentina. Biol. Invas. 10, 1333–1344.
- Pescador, M., Sanguinetti, J., Pastore, H., Peris, S., 2009. Expansion of the introduced wild boar (*Sus scrofa*) in the Andean region, Argentinean Patagonia. Galemys 21, 121–132.
- Risch, A.C., Wirthner, S., Busse, M.D., Page-Dumroese, D.S., Schütz, M., 2010. Grubbing by wild boar (*Sus scrofa*) and its impact on hardwood forest soil CO₂ emissions in Switzerland. Oecologia 164, 773–784.
- Roig, F., Roig-Junent, S., Corbalán, V., 2009. Biogeography of the Monte Desert. J. Arid Environ. 73, 164–172.
- Rundel, P.W., Villagra, P.E., Dillon, M.O., Roig-Juñent, S., Debandi, G., 2007. Arid and semi-arid ecosystems. In: Veblen, T.T., Young, K., Orme, A.E. (Eds.), The Physical Geography of South America. Oxford University Press, pp. 158–183.
- Sanguinetti, J., Kitzberger, T., 2010. Factors controlling seed predation by rodents and non-native Sus scrofa in Araucaria araucana forests: potential effects on seedling establishment. Biol. Invas. 12, 689–706.
- Singer, F.J., Swank, W.T., Clebsch, E.E.C., 1984. Effects of wild pig rooting in a deciduous forest. J. Wildl. Manage. 48, 464–473.Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Mar-
- Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Marion, G., O'Connor, M., Petanidou, T., Peterson, K., Potts, S., Pritchard, H., Pysek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M., Vighi, M., Zobel, M., Kühn, I., 2005. ALARM (Assessing LArge-scale Environmental Risks for biodiversity with tested Methods). Gaia 14, 69–72.
- Seward, N.W., Vercauteren, K.C., Witmer, G.W., Engeman, R.M., 2004. Feral swine impacts on agriculture and the environment. Sheep Goat Res. J. 19, 34–40. Sherrod, S.K., Seastedt, T.R., 2001. Effects of the northern pocket gopher (*Thomomys*)
- Sherrod, S.K., Seastedt, T.R., 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55, 195–218.
- Sousa, W., 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15, 353–391.
- Stasi, C.R., Medero, M.N., 1983. Estudio ecológico y bromatológico de Pitraea cuneatoovata (Cav.) Caro, una especie forrajera del "Monte" mendocino y sanjuanino. Deserta 7, 7–11.
- Tierney, T.A., Cushman, J.H., 2006. Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. Biol. Invas. 8, 1073–1089.
- Villagra, P.E., Defossé, G.E., del Valle, H.F., Tabeni, S., Rostagno, M., Cesca, E., Abraham, E., 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. J. Arid Environ. 73, 202–211.
- Vitousek, P., D'Antonio, C., Loope, L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. N.Z. J. Ecol. 21, 1–16.
- Williamson, M., 1996. Biological Invasions. Chapman & Hall, London, United Kingdom.
- Wilson, C.J., 2004. Rooting damage to farmland in Dorset, southern England, caused by feral wild boar Sus scrofa. Mammal Rev. 34 (4), 331–335.
- Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, New Jersey.

306

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