Wild boar rooting impacts soil function differently in different plant community types

4 authors:

M. Noelia Barrios-Garcia
University of Vermont
42 PUBLICATIONS **1,953** CITATIONS

SEE PROFILE

Daniel Simberloff
University of Tennessee at Knoxville
371 PUBLICATIONS **66,029** CITATIONS

SEE PROFILE

Marina Gonzalez Polo
National University of Comahue
40 PUBLICATIONS **757** CITATIONS

SEE PROFILE

Aimee Classen
University of Michigan
195 PUBLICATIONS **17,256** CITATIONS

SEE PROFILE

ORIGINAL PAPER

Wild boar rooting impacts soil function differently in different plant community types

M. Noelia Barrios-Garcia[ID] ·
**Marina Gonzalez-Polo · Daniel Simberloff ·
Aimée T. Classen**

Abstract While numerous studies focus on the ecosystem effects of invasive mammals, few explore the causal mechanisms of such effects. Wild boar is one of the most widely introduced invasive mammal species in the world. By overturning extensive areas of vegetation and soil to feed on belowground resources, wild boar alter the soil food web and thus many microbial-mediated soil processes. Here, we take advantage of a long-term, 8-year, wild boar exclosure experiment across three plant community types in Patagonia, Argentina to explore how wild boar impact soil communities and their potential function. Previous work in this experimental system found that wild boar significantly impacted litter decomposition in the field, but it remained unclear if this effect was mediated through changes in abiotic or biotic soil properties. To explore both the abiotic and biotic drivers of decomposition, we measured soil moisture, soil temperature, soil bulk density, and soil respiration as well as soil micro-arthropod richness and abundance, earthworm abundance, and microbial biomass inside and outside of 10 exclosures in each of three plant community types. To assess potential microbial activity, we measured potential decomposition rates, substrate-induced respiration, and soil microbial enzyme activity. Rooting decreased soil moisture by 18% across plant communities, and soil respiration by 30% in *Nothofagus* and *Austrocedrus* forests. Additionally, rooting decreased soil micro-arthropod richness and abundance by ~ 80% in shrublands. However, rooting had no effect on soil potential microbial activity. Together, our results suggest that changes in both abiotic and biotic soil factors likely mediate observed wild boar impact on decomposition rates. Overall, we show that wild boar rooting alters soil functioning, but the pathway of impact varies by plant community, suggesting that wild boar impacts on native ecosystems can be difficult to predict.

M. N. Barrios-Garcia (✉)
CONICET, CENAC-APN, Universidad Nacional del Comahue (CRUB), Fagnano 244, 8400 Bariloche, Argentina
e-mail: noeliabarrios@gmail.com

M. N. Barrios-Garcia
Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA

M. Gonzalez-Polo
Grupo de Suelos, Instituto de Investigaciones en Biodiversidad Y Medio Ambiente (INIBIOMA), CONICET–Universidad Nacional del Comahue (CRUB), Quintral 1250, 8400 Bariloche, Argentina

D. Simberloff
Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, USA

A. T. Classen
Department of Ecology and Evolutionary Biology, University of Michigan, 1105 North University Ave, Ann Arbor, MI 48109-1085, USA

Introduction

Biological invasions are a pervasive driver of global change (Assessment 2005), and a growing number of studies find that invasive species radically transform natural systems at ecosystem scales (Ehrenfeld 2010; Simberloff et al 2013; Wardle and Peltzer 2017). Ecosystem impacts are greatest when the introduced species differs substantially from trophically equivalent species in the native community (Ehrenfeld 2010; Wardle and Peltzer 2017). For example, introduction of American beaver (*Castor canandensis*) in Patagonia completely reshaped forests into meadow-like ecosystems (Lizarralde et al. 1996). Dam construction by beavers alters water flow and nutrient dynamics, increasing soil organic nitrogen, phosphorus, and carbon (Lizarralde et al. 1996; Anderson et al. 2014) across the landscape. These changes subsequently influence macro-invertebrate communities by simplifying their assemblages and food web structure (Anderson and Rosemond 2007 and 2010). While many examples of invasive mammal ecosystem-level impacts are striking, the vast majority of invasive species impacts on ecosystem processes are mediated through shifts in the biotic and abiotic factors of native communities (Wardle et al. 2012; Kardol et al. 2014). However, unraveling the causal mechanisms between invasive species impacts and the changes in biotic and abiotic factors is challenging (Gutiérrez et al., 2014; Wardle and Peltzer 2017). In addition, most studies exploring invasive species impacts on ecosystem processes have focused on plant invasions, and considerably less is known about the impacts of invasive animals on soil properties and associated processes (Ehrenfeld 2010; Wardle et al. 2012).

Animal invasions can cause soil-mediated impacts through several mechanisms (Ehrenfeld 2010). For example, invasive ungulate trampling in New Zealand forests reduces plant growth by influencing both soil abiotic and biotic properties such as bulk density and arbuscular mycorrhizal colonization (Kardol et al. 2014). Likewise, animal invasions can alter key ecosystem processes like organic matter decomposition rates. Litter decomposition determines soil nutrient dynamics and is controlled by climate, litter chemical composition, and soil organisms (Coûteaux et al. 1995). Previous studies have shown that animal invasions can alter decomposition rates through abiotic and biotic pathways. For example, forest defoliation by the invasive hemlock woolly adelgid (*Adelges tsugae*) in the eastern United States alters forest microclimatic conditions, reducing soil moisture and consequently retarding mass loss (Cobb et al. 2006). Alternatively, animal invasions can alter decomposition rates through biotic pathways. For example, Li et al. (2002) found that invasion by the earthworm *Lumbricus rubellus* in hardwood forests increases soil microbial biomass and respiration by enhancing organic carbon availability via processing and mixing of litter. However, corresponding studies of such soil-mediated effects by large mammalian herbivores are very limited.

Here, we assess the mechanisms by which a widespread invasive ungulate can alter decomposition rates. Wild boar (*Sus scrofa*) are native to Eurasia but have been introduced in all continents except Antarctica (Long 2003). While foraging on belowground resources, wild boar disturb extensive areas of vegetation and soil. This rooting has many impacts on plant and animal communities as well as on soil properties worldwide (Barrios-Garcia and Ballari 2012). For example, in a previous study we found that rooting altered plant community composition and structure by reducing plant biomass by a factor of 3.8, by decreasing grass and herb cover, and by promoting invasion by other introduced plants (Barrios-Garcia and Simberloff 2013; Barrios-Garcia et al. 2014). Similarly, we found that rooting by wild boar reduced litter decomposition rates (Barrios-Garcia et al. 2014). However, it is unclear whether this effect on the decomposition rate is mediated through changes in abiotic or biotic soil properties.

Prior work suggests that wild boar negatively impact soil communities and function. For example, when wild boar were removed from a Hawaiian forest via exclusion, soil bacterial and macroinvertebrates diversity increased (Wehr et al. 2019, 2020). In the same Hawaiian forest wild boar exclusion changed soil physical and chemical properties by increasing soil porosity, soil inorganic nitrogen content and mineralization; and decreasing soil bulk density, soil moisture, and pH (Long et al. 2017). While these studies are compelling, none of the previous studies explored how changes in the soil communities might

alter other ecosystem processes such as litter decomposition rates.

Using a large-scale wild boar exclosure experiment in Patagonia we tested the influence of rooting on soil abiotic and biotic properties in mediating decomposition rates. Specifically, we addressed (1) how does wild boar rooting affect soil abiotic factors? (2) How does wild boar rooting affect the soil decomposer community? To answer these questions, we measured soil abiotic factors inside and outside the exclosures in the field and collected soil samples to measure soil fauna community and soil microbial activity in the laboratory. We predicted that wild boar rooting would alter soil abiotic and biotic factors, reducing soil moisture, fauna richness and abundance, and soil microbial activity.

Methods

This study was conducted on Isla Victoria, an island of 3710 ha in Nahuel Huapi Lake in northwestern Patagonia, Argentina (40° 57′ S, 71° 33′ W). Soils are young Andisols derived from postglacial volcanic ashes (Ayesa et al. 2002), mean annual precipitation is 1700 mm, and mean annual temperature is 8 °C. There are three dominant plant communities on the island: cypress forests of *Austrocedrus chilensis* (D.Don) Florin & Boutlelje (Cupressaceae), southern beech forests of *Nothofagus dombeyi* Blume (Fagaceae), and shrublands co-dominated by *Lomatia hirsuta* (Lam.) Diels (Proteaceae) and *Maytenus boaria* Molina (Celastraceae). The understory plant composition is dominated by woody shrubs such as *Schinus patagonicus* (Phil.) I.M.Johnst. ex Cabrera (Anacardiaceae) and *Berberis darwinii* Hook (Berberidaceae), herbs, and graminoids in different proportions depending on the dominant tree community. Specifically, shrub cover is greater in *Austrocedrus* forests than in *Nothofagus* forests and shrublands (25.5 ± 1.88%, 20.18 ± 1.79%, and 19.76 ± 2.46%, respectively), herb cover is twofold greater in shrublands than in *Nothofagus* and *Austrocedrus* forests (29.12 ± 1.87%, 14.38 ± 1.27%, and 13.8 ± 1.42%, respectively), and grass cover is 11-fold greater in shrublands and *Austrocedrus* forests than in *Nothofagus* forests (44.96 ± 2.99%, 43.72 ± 2.81%, and 3.72 ± 1.02%, respectively, Barrios-Garcia et al. 2014). These plant communities are close to each

other, but *Nothofagus* forests dominate in mesic areas by the shores of the island, *Austrocedrus* forests dominate in xeric areas on hills, and shrublands are successional (Veblen and Lorenz 1987). Wild boar colonized Isla Victoria in 1999 (Simberloff et al. 2003) and currently attain high densities across the island (M. N. Barrios-Garcia personal observation). The high abundance of wild boar results from the complete lack of predators on the island and the limited hunting efforts to control their population.

In 2008, we established an exclosure experiment to test how foraging by boar alters the structure and function of forested ecosystems (see details in Barrios-Garcia et al. 2014). Each exclosure is 11m² fenced with 1 m high woven wire and a strand of barbed wire at ground level along the perimeter to prevent boar from prying up the fencing (Tierney and Cushman 2006). We established 10 circular exclosures in each of the three dominant plant communities—*Austrocedrus* forests, *Nothofagus* forests, and shrublands—in areas with no visible rooting activity (N = 30). As controls, we established four boar-access plots (11m², 0.5 m apart) adjacent to each exclosure to increase the likelihood of capturing soil disturbance. Exclosures were established in groups of 2 or 3, and the distance between groups varied from 100 m to 5 km.

Abiotic factors

In November 2016 we collected two soil samples with soil cores (0–10 cm depth, 5 cm diameter) inside and outside of each exclosure in freshly wild boar disturbed areas. We focused our sampling on exclosures that were paired with fresh wild boar disturbance, thus collecting 10 paired-samples in *Austrocedrus* forest, 9 paired-samples in *Nothofagus* forest, and 7 paired-samples in shrublands. Soil samples from within each exclosure or control plot were combined and stored in sealed plastic bags transported immediately to the laboratory, then sieved through a 2 mm mesh for biotic factor measurements. Additionally, an intact soil core (0–10 cm depth) was collected to measure soil bulk density. At the time of soil sampling, we measured soil temperature (0–10 cm depth) and determined volumetric soil moisture (0–10 cm depth) using an EGM-4 Environmental Gas Monitor (PP Systems, USA) inside and outside of each exclosure.

Field biotic factors

Soil fauna—Microarthropods and earthworms are both important members of the decomposition food web (Coûteaux et al. 1995) and shifts in their abundance or diversity can indicate shifts in long-term soil carbon storage (Wiesmeier et al. 2019). To investigate the effect of rooting on soil microarthropod abundance, richness, and composition we collected two soil cores in February 2014 (0–10 cm depth, 3 cm diameter) inside and outside of each exclosure in areas freshly disturbed by wild boar (7 paired-samples in *Austrocedrus* forest, 9 in *Nothofagus* forest and 7 in shrublands). We extracted microarthropods from soil samples using high-gradient Tullgren funnels (extracted for 72 h; Merchant and Crossley, 1970). Tullgren funnels with 25 W light bulbs dried the soil cores, which induced the microarthropods to migrate downward into vials with 70% ethanol. All microarthropod specimens were counted (abundance) and identified to morphospecies (diversity) using taxonomic guides (Bugguide. net, Palacios-Vargas et al., 2014). Additionally, we sampled earthworms from a 25×25 cm quadrat placed inside and outside five exclosures in each plant community (n = 15). Soils were collected by shovel to a depth of 25 cm and placed in a plastic sheet. We sorted earthworms by hand, counted them, and weighed them with a spring scale.

Microbial respiration and biomass—In the field, we measured soil respiration using an EGM-4 Environmental Gas Monitor with a closed system soil respiration chamber (PP Systems, USA) inside and outside of each exclosure in areas freshly disturbed by wild boar. Additionally, in the laboratory we measured microbial biomass-carbon using the chloroform fumigation–extraction technique (Vance et al. 1987). Briefly, collected soils (30 g) were fumigated with ethanol–free chloroform for 24 h. We extracted fumigated and unfumigated soil samples with K_2SO_4 (0.5 M) and analyzed each sample for carbon using dichromate oxidation. Microbial biomass-carbon was calculated as fumigated minus unfumigated carbon concentrations. A conversion factor of 0.45 (Kc) was used to convert extracted carbon to microbial biomass-carbon.

Soil potential activity

Lab decomposition (standard substrate)—To control for the effect of climate and to assess potential microbial decomposition, we conducted a laboratory decomposition incubation. We brought soils samples (30 g) up to field-holding capacity by adding 20 mL of water. Each soil sample was placed in an individual Petri dish and a pre-weighed 7 cm diameter filter paper (Munktell, Sweden) was placed on the soil surface. Each Petri dish was sealed with tape and incubated for 12 weeks at a constant laboratory temperature (25 °C). At the end of the 12-week incubation, we removed the filter papers, oven-dried them (48 h at 60 °C), and weighed them. Then, we ashed the filter paper disks in a muffle furnace at 550 °C for 6 h to determine percent mass remaining on an ash-free oven-dry basis.

Microbial activity—To understand how microbial activity may contribute to shifts in decomposition with wild boar activity, we measured potential microbial activity using substrate-induced respiration (SIR) and soil enzyme activity. To measure SIR we amended soil samples (3 g) with a glucose solution (5 mg g^{-1} soil) and incubated them at 25 °C for 2 h in falcon tubes (West and Sparling 1986). We then measured CO_2 production in each sample by sampling 5 mL of the headspace gas with an EGM-4 Environmental Gas Monitor (PP Systems, USA). We assessed potential soil enzyme activity of three enzymes: beta-glucosidase, leucine-aminopeptidase, and acid phosphatase that break down cellulose, amino acids, and release phosphorous, respectively. We created soil-to-water suspensions (1:10), and 1 mL of homogenate was combined with 1 mL of each enzyme substrate and shaken at 25 °C for 2 h (beta-glucosidase and leucine-aminopeptidase) or 1 h (acid phosphatase). Substrates were 5 mM pNP-beta-D-glucopyranoside for beta-glucosidase, 2 mM leucin p-nitroanilide for leucin aminopeptidase (TRIS buffer, pH 8), and 5 mM pNP-phosphate for acid phosphatase (acetate buffer, pH 5). The reactions were stopped by adding NaOH, then samples were centrifuged at 3000 rev min^{-1}, and supernatant absorbance was measured at 410 nm with a spectrometer (Sinsabaugh et al. 1999).

Data analyses

We used two-way ANOVAs to test for the effects of wild boar rooting, plant community type, and their interaction on soil temperature and moisture, soil bulk density, soil respiration, microbial biomass, lab-potential decomposition rate, and soil enzyme activity. Soil moisture, bulk density, soil respiration, and beta-glucosidase activity were log-transformed, and % mass remaining were logit-transformed (Warton and Hui 2011) to meet normality assumptions. We analyzed the effects of wild boar rooting, plant community type, and their interaction on soil micro-arthropod richness and abundance with separate GLM models with Poisson distribution. Additionally, we tested the effects of wild boar rooting, plant community type, and their interaction on micro-arthropod community composition with PERMANOVA using a Bray–Curtis dissimilarity matrix on log-transformed abundance data (Primer-E). All two-way ANOVAs and GLMs were conducted on JMP Pro 11 statistical software with alpha set a priori as $\alpha < 0.05$ (SAS Institute, Pacific Grove, CA, USA, 2001).

Results

Impact on abiotic factors

Wild boar disturbance significantly decreased volumetric soil moisture (two-way ANOVA, $p = 0.0068$, $F_{5,45} = 3.77$) but had no effect on soil temperature or bulk density, which differed only among plant communities (two-way ANOVA, $p = 0.0106$, $F_{5,46} = 3.46$ and $p < 0.001$, $F_{5,43} = 25.41$ respectively, Table 1). Specifically, soil temperature was ~1 °C greater in *Austrocedrus* forest and shrubland compared to

Nothofagus forest, and bulk density was higher in shrublands, intermediate in *Austrocedrus* forest, and lower in *Nothofagus* forest (Table 1).

Impact on field biotic factors

Soil fauna—We recorded 144 individuals belonging to 18 morphospecies; Acari accounted for half of the total microarthropod abundance. We also identified other arachnids, dipteran larvae, collembolans, centipedes, nematodes, and annelids. Overall, arthropod richness decreased by 75% in wild boar-rooted plots in shrublands and varied among plant communities (GLM $p = 0.0371$, $\chi^2 = 11.83$, Fig. 1). Similarly, arthropod abundance varied with community, rooting, and their interaction (GLM $p < 0.0001$, $\chi^2 = 29.09$). Specifically, rooting by boar decreased arthropod abundance by 88% in shrublands (Fig. 1). These changes, nevertheless, did not alter overall soil arthropod community composition (PERMANOVA $p > 0.75$). Additionally, we found only 24 earthworms, 19 individuals inside the exclosures in shrublands, 3 in rooted plots in shrublands, 1 in an exclosure in *Austrocedrus* forest, and 1 in a rooted plot in *Austrocedrus* forest.

Microbial respiration and biomass—Rooting decreased soil respiration in the field by 30% in *Nothofagus* and *Austrocedrus* forests (two-way ANOVA, $p = 0.0036$, $F_{5,46} = 4.18$, Fig. 2a) but had no effect on microbial biomass (two-way ANOVA, $p > 0.05$, Table 2).

Impact on soil potential activity

Lab decomposition (standard substrate)—We found no effect of rooting on lab-incubated standard-substrate decomposition rates, which differed

Table 1 Soil abiotic factors inside and outside wild boar exclosures in each of the three plant communities. The values indicate means ± SE, lowercase letters show significant differences

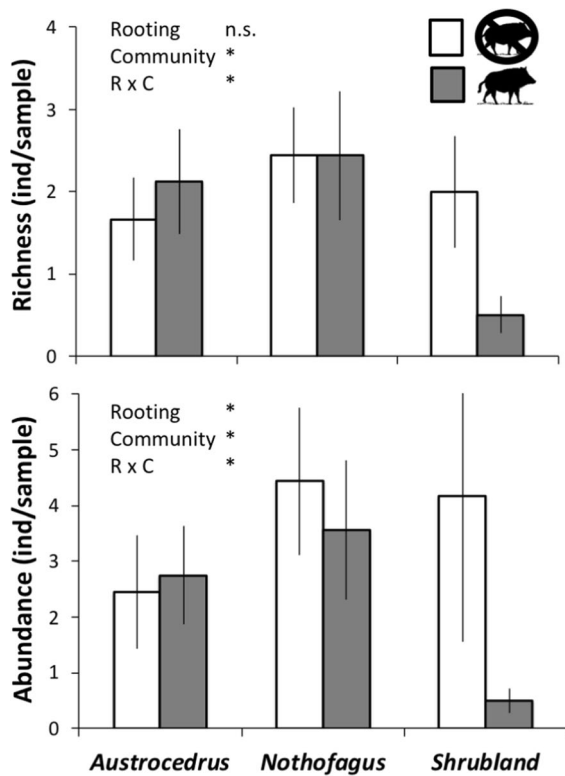| Plant community	Treatment	Soil moisture (%)	Soil temperature (°C)	Bulk density (g/cm^3)
Austrocedrus forest	No rooting	14.83 (0.78) a	14.22 (0.40) a	0.51 (0.01) b
	Rooting	11.70 (0.61) b	13.88 (0.35) a	0.56 (0.02) b
Nothofagus forest	No rooting	13.13 (0.32) a	12.55 (0.24) b	0.47 (0.02) c
	Rooting	10.82 (0.40) b	13.00 (0.33) b	0.48 (0.01) c
Shrubland	No rooting	13.66 (1.68) a	14.33 (0.66) a	0.69 (0.03) a
	Rooting	11.80 (1.19) b	14.50 (0.67) a	0.73 (0.01) a

Fig. 1 Results of the GLMs addressing effects of wild boar rooting, plant community, and their interaction (R x C) on soil arthropod richness and abundance. Values indicate means ± SE, * imply significant effects

only among plant communities (two-way ANOVA $p = 0.0389$, $F_{5,44} = 2.62$). Specifically, decomposition rate was ~15% greater in *Nothofagus* forests than in *Austrocedrus* forests and shrublands (Fig. 2b).

Microbial activity—We found no effect of rooting on substrate-induced respiration in the lab, which also differed (marginally) only among plant communities (two-way ANOVA, $p = 0.0923$, $F_{5,46} = 2.06$, Fig. 2c). Consistently, we detected no effect of rooting on any soil enzyme activity, of which only acid-phosphatase and leucin-aminopeptidase differed among plant communities (two-way ANOVA $p = 0.0203$, $F_{5,49} = 3.00$, and $p < 0.0001$, $F_{5,50} = 6.59$ respectively, Table 2).

Discussion

Our experiment shows that rooting by wild boar induces changes in soil abiotic and biotic properties, which then mediate decomposition rates. Rooting
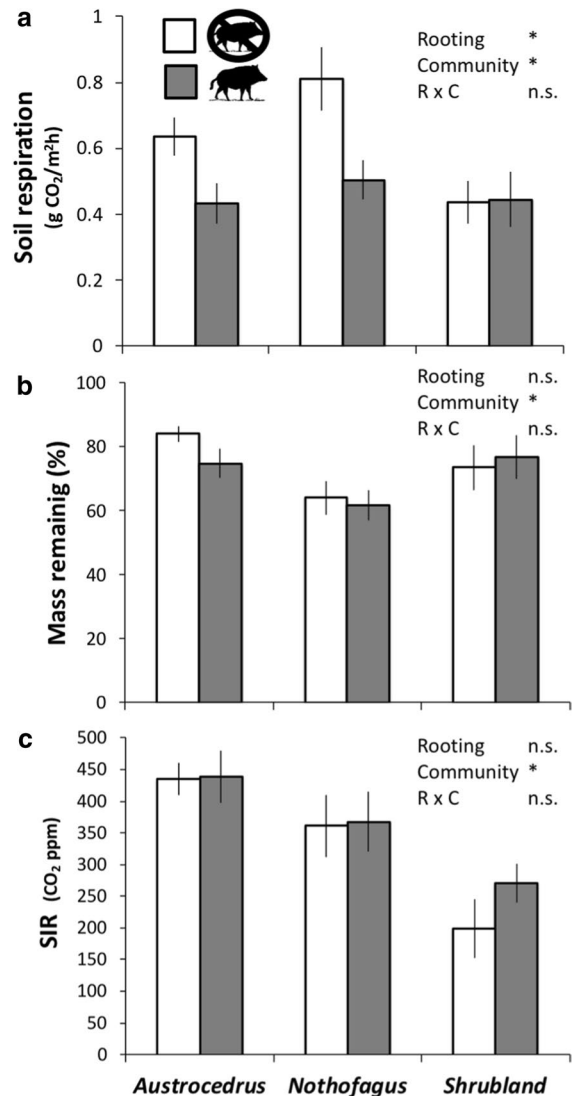

Fig. 2 Results of the ANOVAs addressing effects of wild boar rooting, plant community, and their interaction (R x C) on **a** soil respiration in the field, **b** decomposition rate in the laboratory, and **c** substrate-induced respiration. Values indicate means ± SE, * imply significant effects

decreased soil moisture across plant communities and soil respiration rates in *Nothofagus* and *Austrocedrus* forests but had no effect on microbial biomass-C, substrate-induced respiration, or soil microbial enzyme activity. Interestingly, we found a stronger signal of wild boar activity on field measures than on potential lab measures, indicating that boar activity impacts ecosystem function in the field by changing soil moisture, a factor that is controlled in the

Table 2 Soil biotic factors inside and outside the wild boar exclosures in each of the three plant communities. The values indicate means $\pm$ SE

Plant community	Treatment	Beta-glucosidase ($\mu mol/m^2h$)	Acid phosphatase ($\mu mol/m^2h$)	Leucin-aminopeptidase ($\mu mol/m^2h$)	Microbial biomass C (μg de C/cm^3)
Austrocedrus forest	No rooting	103.39 (10.03) a	181.11 (15.23) b	82.16 (6.75) a	21.65 (3.37) a
	Rooting	125.07 (13.22) a	205.55 (20.74) b	102.9 (10.36) a	20.71 (3.79) a
Nothofagus forest	No rooting	105.34 (5.92) a	319.54 (25.31) a	83.81 (8.04) ab	21.02 (2.27) a
	Rooting	100.06 (9.58) a	292.01 (20.80) a	89.67 (7.64) ab	20.05 (3.11) a
Shrubland	No rooting	126.03 (24.03) a	349.81 (31.57) a	66.91 (7.36) b	27.02 (3.41) a
	Rooting	123.80 (18.47) a	308.68 (49.50) a	65.73 (4.73) b	22.62 (3.71) a

lab environment. Additionally, we found that wild boar rooting decreased soil micro-arthropod richness and abundance by ~80% in shrublands, indicating that rooting reduces the diversity and abundance of important soil food web members in some plant communities, a pattern that may feedback to affect soil function. Together, these results provide evidence that wild boar impact both the abiotic and the biotic factors that mediate ecosystem processes in diverse ecosystem types.

The pathways by which wild boar alter decomposition rates matched those assessed by previous studies looking at the direct impacts of wild boar on soil properties. For example, Risch et al. (2010) found that rooting significantly reduced soil moisture and increased temperature in Swiss hardwood forests. Similarly, in grasslands in Spain (Bueno et al. 2013) and a pine forest in Poland (Sławski and Sławska 2020), wild boar rooting reduced soil moisture. However, in our study, soil moisture changes did not lead to a change in potential microbial activity in the lab. This result was surprising because soil moisture is an important driver of microbial community structure and function, and we expected moisture-driven changes in the communities in the field to mirror results for assays in the lab and to impact decomposition rates (Fanin et al. 2019). The young volcanic soils at our site may have the capacity to buffer the impacts of wild boar because they physically and chemically protect soil organic matter from microbial decomposition (Shoji et al. 1994)—thus the microbial communities at our sites may be resource-limited and unable to respond to the boar disturbance. While we do not know the exact mechanism driving this pattern at our sites, our findings are inline with those from other studies in a Swiss hardwood forest (Wirthner

et al. 2011) and a conifer-angiosperm forest in New Zealand (Parkes et al. 2017). By contrast, three other studies found increased soil respiration rates in disturbed plots compared to undisturbed plots in hardwood forests of Switzerland and China, and Monte desert in Argentina, respectively (Risch et al. 2010, Cuevas et al. 2012, Liu et al. 2020). These contrasting results might be related to the use of different field and laboratory methods. That is, we found differences in soil respiration rates in the field using a CO_2 analyzer, as did Risch et al. (2010) and Liu et al. (2020), but we found no differences in the laboratory incubations, similar to Wirthner et al. (2011) and Parkes et al. (2017). Laboratory incubations measure potential microbial activity in the absence of roots and under ideal soil moisture and temperatures, whereas field measurements reflect more realistic rates of soil activity that includes microbial communities, roots as well as heterogeneity in soil texture, soil moisture, and soil temperatures. Wild boar diet is ~90% plant material (Ballari and Barrios-Garcia, 2014), and thus boar rooting significantly reduces belowground biomass. Further research should explore the mechanisms by which wild boar alter soil respiration rates at individual field sites, as well as at field sites in different ecosystems, and the ecosystem properties that underlie these divergent responses.

We found that rooting by wild boar reduced soil arthropod richness and abundance in one plant community–shrublands. While several studies have identified the impact of invasive species on soil fauna, only a handful studies have explicitly focused on wild boar. Vtorov (1993) found that microarthropod density, mostly collembolans, doubled after wild boar were excluded from fenced areas for 7 years in Hawaii, USA. Similarly, Carpio et al.

(2014) found that wild boar density was negatively related to invertebrate richness and abundance in a Mediterranean ecosystem, and Slawski and Slawska (2020) found that rooting in a Polish forest also reduced collembolan abundance and richness. Interestingly, other studies that focused on soil macro-arthropod species found that rooting increased the abundance of carabid beetles (Fagiani et al. 2014; Wehr et al. 2019) and earthworms (Wehr et al. 2019). Thus, wild boar can have positive and negative impacts on soil communities. While these patterns are interesting in their own right, none of the previous studies explored how changes in soil organisms might also change soil function.

Perhaps not surprisingly, the impact of wild boar was context-dependent and varied with the plant communities on Isla Victoria. Wild boar rooting altered soil respiration in forested communities but not in shrublands, while it altered soil arthropod richness and abundance in shrublands but not in forested communities. These differential impacts across plant communities could be related to the inherent properties of the plant communities. For example, shrubland soils have a coarser texture and contain 30% less soil carbon than forested soils (Barrios-Garcia et al. 2014). These differences in soil properties could explain why rooting did not affect soil respiration in shrublands. Additionally, shrublands are successional communities (Veblen and Lorenz 1987), with open canopy and almost 100% understory cover with a high diversity of shrubs, herbs, and grasses compared to *Austrocedrus* forests with 80% understory cover and *Nothofagus* forest with only 40% understory cover (Barrios-Garcia et al. 2014). Previous studies found a positive relationship between plant diversity and cover and soil fauna, suggesting that could be the case with our study site (Siemann et al 1999; Meloni et al. 2020).

To conclude, our study exploring multiple pathways by which invasive animals can influence decomposition rates provides evidence that both biotic and abiotic factors are important, but some are more relevant than others depending on the plant community. These results show that impacts of invasive mammals are complex and difficult to predict and that a better understanding of the underlying mechanisms by which invasive mammals alter native ecosystems is essential for reliably predicting large-scale and long-term consequences of invasions on ecosystem processes (Wardle et al. 2001; Wardle and Peltzer 2017).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on request.

References

Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologia 154:141–153

Anderson CB, Rosemond AD (2010) Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. Hydrobiologia 652:349–361

Anderson CB, Vanessa Lencinas M, Wallem PK, Valenzuela AE, Simanonok MP, Martinez Pastur G (2014) Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. Divers Distrib 20:214–222

Assess, M.E, (2005) Ecosystems and human well-being: synthesis. Island Press

Ayesa JA, Lopez CR, Bran DE, Umana FJ, and Lagorio PA (2002) Cartografía biofísica de la Patagonia Norte. INTA Estación Experimental Agropecuaria Bariloche, Pan, Prodesar.

Ballari SA, Barrios-Garcia MN (2014) A review of wild boar (*Sus scrofa*) diet and factors affecting food selection in the native and introduced ranges. Mammal Rev 44:124–134

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol Invasions 14:2283–2300

Barrios-Garcia MN, Simberloff D (2013) Linking the pattern to the mechanism: how an introduced mammal facilitates plant invasions. Austral Ecol 38:884–890

Barrios-Garcia MN, Classen AT, Simberloff D (2014) Disparate responses of above-and belowground properties to soil disturbance by an invasive mammal. Ecosphere 5:art44

Bueno CG, Azorín J, Gómez-García D, Alados CL, Badía D (2013) Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. Plant Soil 373(1–2):243–256

Carpio AJ, Castro-López J, Guerrero-Casado J, Ruiz-Aizpurua L, Vicente J, Tortosa FS (2014) Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem. Anim Biodivers Conserv 37:115–125

Cobb RC, Orwig DA, Currie S (2006) Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid infestations. Can J for Res 36:1331–1341

Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and liter quality. Trends Ecol Evol 10:63–66

Cuevas MF, Mastrantonio L, Ojeda RA, Jaksic FM (2012) Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. Mammal Biol 77(4):299–306

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80

Fagiani S, Fipaldini D, Santarelli L, Burrascano S, Del Vico E, Giarrizzo E, Mei M, Vigna TA, Boitani L, Mortelliti A (2014) Monitoring protocols for the evaluation of the impact of wild boar (*Sus scrofa*) rooting on plants and animals in forest ecosystems. Hystrix Italian J Mammal 25(1):31–38

Fanin N, Bezaud S, Sarneel JM, Cecchini S, Nicolas M, Augusto L (2019) Relative importance of climate, soil and plant functional traits during the early decomposition stage of standardized litter. Ecosystems 23:1–15

Gutiérrez JL, Jones CG, Sousa R (2014) Toward an integrated ecosystem perspective of invasive species impacts. Acta Oecologica 54:131–138

Kardol P, Dickie IA, John MGS, Husheer SW, Bonner KI, Bellingham PJ, Wardle DA (2014) Soil-mediated effects of invasive ungulates on native tree seedlings. J Ecol 102:622–631

Li X, Fisk MC, Fahey TJ, Bohlen PJ (2002) Influence of earthworm invasion on soil microbial biomass and activity in a northern hardwood forest. Soil Biol Biochem 34:1929–1937

Liu Y, Liu X, Yang Z, Li G, Liu S (2020) Wild boar grubbing causes organic carbon loss from both top-and subsoil in an oak forest in central China. For Ecol Manag 464:118059

Lizarralde M, Deferrari G, Alvarez SE, Escobar JM (1996) Effects of beaver (*Castor canadensis*) on the nutrient dynamics of the southern beech forest of Tierra del Fuego (Argentina). Ecol Austral 6(2):101–105

Long JL (2003) Introduced mammals of the world: their history distribution and influence. CSIRO, Collingwood

Long MS, Litton CM, Giardina CP, Deenik J, Cole RJ, Sparks JP (2017) Impact of nonnative feral pig removal on soil structure and nutrient availability in Hawaiian tropical montane wet forests. Biol Invasions 19:749–763

Meloni F, Civieta BF, Zaragoza JA, Lourdes Moraza M, Bautista S (2020) Vegetation pattern modulates ground arthropod diversity in semi-arid Mediterranean steppes. Insects 11(1):59

Parkes JP, Easdale TA, Williamson WM, Forsyth DM (2017) Causes and consequences of ground disturbance by feral pigs (*Sus scrofa*) in a lowland New Zealand conifer–angiosperm forest. N Z J Ecol 39(1):34–42

Risch AC, Wirthner S, Busse MD, Page-Dumroese DS, Schütz M (2010) Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. Oecologia 164:773–784

Shoji S, Nanzyo M, Dahlgren RA (1994) Volcanic ash soils: genesis properties and utilization. Elsevier, Amsterdam

Siemann E, Haarstad J, Tilman D (1999) Dynamics of plant and arthropod diversity during old field succession. Ecography 22(4):406–414

Simberloff D, Relva MA, Nuñez M (2003) Introduced species and management of a Nothofagus/Austrocedrus forest. Environ Manag 31(2):263–275

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Sinsabaugh RL, Klug MJ, Collins HP, Yeager PE, Petersen SO (1999) Characterizing soil microbial communities. In: Robertson PG, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. Oxford University Press, New York, pp 318–348

Sławski M, Sławska M (2020) Collembolan assemblages response to wild boars (*Sus scrofa* L.) rooting in pine forest soil. Forests 11(11):1123

Tierney TA, Cushman JH (2006) Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. Biol Invasions 8:1073–1089

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass. Soil Biol Biochem 19:703–707

Vargas JGP, Recamier BEM, De Oyarzabal ALDI (2014) Guía ilustrada para los artrópodos edáficos. La prensa de Ciencias, Mexico, p 84

Veblen TT, Lorenz DC (1987) Post-fire stand development of *Austrocedrus-Nothofagus* forests in northern Patagonia. Vegetatio 71(2):113–126

Vtorov IP (1993) Feral pig removal: effects on soil microarthropods in a Hawaiian rain forest. J Wildl Manag 57:875–880

Wardle DA, Peltzer DA (2017) Impacts of invasive biota in forest ecosystems in an aboveground–belowground context. Biol Invasions 19:3301–3316

Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecol Monogr 71:587–614

Wardle DA, Bellingham PJ, Fukami T, Bonner KI (2012) Soil-mediated indirect impacts of an invasive predator on plant growth. Biol Let 8:574–577

Warton DI, Hui FK (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10

Wehr NH, Kinney KM, Nguyen NH, Giardina CP, Litton CM (2019) Changes in soil bacterial community diversity following the removal of invasive feral pigs from a Hawaiian tropical montane wet forest. Sci Rep 9:14681

Wehr NH, Litton CM, Lincoln NK, Hess SC (2020) Relationships between soil macroinvertebrates and nonnative feral pigs (*Sus scrofa*) in Hawaiian tropical montane wet forests. Biol Invasions 22(2):577–586

West AW, Sparling GP (1986) Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water contents. J Microbiol Methods 5(3–4):177–189

Wiesmeier M, Urbanski L, Hobley E, Lang B, von Lützow M, Marin-Spiotta E, van Wesemael B, Rabot E, Ließ M, Garcia-Franco N, Wollschläger U (2019) Soil organic carbon storage as a key function of soils-a review of drivers and indicators at various scales. Geoderma 333:149–162

Wirthner S, Frey B, Busse MD, Schütz M, Risch AC (2011) Effects of wild boar (*Sus scrofa* L.) rooting on the bacterial community structure in mixed-hardwood forest soils in Switzerland. Eur J Soil Biol 47(5):296–302