

Disparate responses of above- and belowground properties to soil disturbance by an invasive mammal

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Abstract. Introduced mammalian herbivores can negatively affect ecosystem structure and function if they introduce a novel disturbance to an ecosystem. For example, belowground foraging herbivores that bioturbate the soil, may alter process rates and community composition in ecosystems that lack native belowground mammalian foragers. Wild boar (*Sus scrofa*) disturb the soil system and plant community via their rooting behavior in their native range. Given their size and the numbers in their populations, this disturbance can be significant in forested ecosystems. Recently, wild boar were introduced to Patagonian forests lacking native mammalian herbivores that forage belowground. To explore how introduced wild boar might alter forested ecosystems, we conducted a large-scale wild boar exclusion experiment in three different forest types (*Austrocedrus chilensis* forest, *Nothofagus dombeyi* forest, and shrublands). Wild boar presence altered plant composition and structure, reducing plant biomass 3.8-fold and decreasing both grass and herb cover relative to areas where wild boar were excluded. Decomposition rates and soil compaction also declined by 5% in areas where boar had access; however, rooting had no effect on soil nutrient stocks and cycling. Interestingly, there were no differences in wild boar impacts on different forest types. We found that after 3-years of exclusion, belowground foraging by wild boar had a larger impact on plant community structure and biomass than it did on soil nutrient processes.

Key words: herbivory; Patagonia; plant community structure; rooting; soil nutrients; *Sus scrofa*; wild boar.

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INTRODUCTION

Below- and aboveground components of terrestrial ecosystems are linked (Bardgett and Wardle 2010), and extensive research demonstrates that herbivory can influence the feedbacks between above- and belowground components of ecosystems (Hooper et al. 2000, Wardle et al. 2001, Augustine et al. 2003, Bardgett and Wardle 2003). For example, selective browsing by herbivores and the production of secondary defensive

compounds by plants can shift plant communities to well-defended plants with poor litter quality, slowing belowground processes such as N mineralization (Pastor et al. 1993). In most ecosystems, herbivore influences on plant composition are common and plants are adapted to herbivory. However invasive herbivores, especially those introducing novel disturbances, can shift the structure and function of an ecosystem and possibly set the system on a new trajectory (Husheer et al. 2003, Côté et al. 2004). For

example, chronic selective browsing by introduced fallow deer in New Zealand lead to a system dominated by low quality grasses, possibly constraining plant production and influencing soil C and N storage (Wardle et al. 2001). While consumption of aboveground biomass can shift the plant community, some herbivores forage belowground for roots, introducing soil disturbance coupled with plant consumption.

Belowground foraging by mammals maintains the structure and influences the function of ecosystems globally (Andersen 1987, Whitford and Kay 1999, Gutiérrez and Jones 2006). Belowground foraging mammals move and mix soil from different horizons, altering soil properties such as moisture, temperature, compaction and nutrient distribution (Huntly and Reichman 1994). In addition, their activity stimulates microbial activity (Eldridge and Mensinga 2007), accelerates organic matter decomposition (Sherrod and Seastedt 2001), and alters plant community composition and chemistry (Sirotnak and Huntly 2000, Gutiérrez and Jones 2006). For example, pocket gophers (*Thomomys bottae*) can consume 30% of the subterranean net primary productivity leading to reduced soil bulk density, mineralization, and decomposition (Reichman and Seabloom 2002, Canals et al. 2003). Similarly, grizzly bears (*Ursus arctos horribilis*) forage for bulbs, creating a patchy distribution of soil nitrogen availability across the landscape. Hence soil disturbance by bears increases N content 1.3-fold in revegetating glacier lilies, influencing both short- and long-term plant community dynamics and ecosystem nutrient dynamics (Tardiff and Stanford 1998). However, how a novel type of disturbance of an ecosystem by an invasive mammal alters ecosystem function remains largely unexplored.

Invasive species are a major driver of ecosystem-change because they can introduce a novel disturbance in an ecosystem or disrupt important interactions between organisms. For example, predation by introduced rats on seabirds disrupted sea-to-land nutrient transfers, reducing soil fauna abundance and increasing litter decomposition rates on New Zealand islands (Fukami et al. 2006). Similarly, earthworm introduction into US northern hardwood forests increased soil mixing, leading to increased

microbial respiration and C availability relative to uninvaded areas (Li et al. 2002).

Recently, non-native wild boar (*Sus scrofa* L.) have invaded forests in Patagonia, Argentina, and their foraging for roots and soil invertebrates has introduced a novel soil disturbance. In other ecosystems, rooting activity by invasive wild boar altered plant community structure and composition as well as soil nutrient availability (Bratton 1975, Kotanen 1995, Tierney and Cushman 2006); however the consequences of their activity for ecosystem processes such as decomposition and nutrient mineralization remain understudied. The introduction of wild boar to Patagonia provides a natural experiment to test the joint effects of soil disturbance (rooting) and root foraging (herbivory) on below- and aboveground ecosystem components and their interaction across several forest types. Wild boar introduce a novel disturbance in Patagonian ecosystems, as no native species bioturbates the soil while foraging. Thus, the arrival in 1999 of wild boar on Isla Victoria, Patagonia, Argentina allowed us to assess the impact of rooting disturbance accurately, as we are certain that wild boar never affected the areas we identify as undisturbed.

Using a large-scale wild boar exclosure experiment (Fig. 1) across three dominant forest types, we measured how boar activity (both experimental and natural) altered plant and soil properties over time. Specifically, we addressed the response of (1) plant community structure and composition, (2) decomposition rates, and (3) soil properties to rooting through time and across forest types. Because rooting by boar targets roots, disrupts soil structure, and mixes soil horizons, we hypothesized that rooting would: (1) decrease plant cover and alter plant species composition, (2) increase decomposition rates, (3) decrease soil compaction and increase nutrient mineralization, and (4) have a greater impact in nutrient-rich ecosystems. We predicted that soil nutrient pools would increase for two reasons. As boar root and disturb the soil plant biomass and thus plant nutrient uptake would decline leading to an increase in nutrient pools; and soil bioturbation would stimulate the microbial activity and the resulting nutrient mineralization.

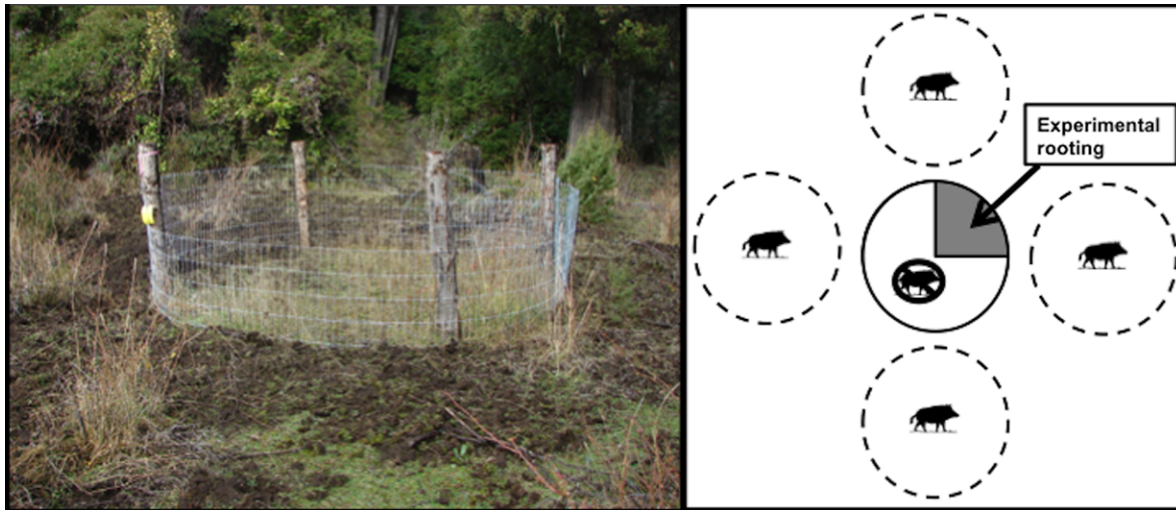


Fig. 1. Wild boar rooting reduces plant abundance, soil compaction, and decomposition rate. The boar enclosure in this photograph is 11 m², 1-m high and was established in 2008. The diagram at the right illustrates the experimental units, with the enclosure in the center and four surrounding open plots where rooting disturbance and plant community changes were recorded.

METHODS

This study was conducted on Isla Victoria (3710 ha), Nahuel Huapi National Park in northwestern Patagonia, Argentina (40°57' S, 71°33' W). Elevation ranges from 765 to 1025 m above sea level, with varied topography including flats, shallow valleys, and hills. Mean annual precipitation is 1700 mm, and mean annual temperature is 8°C. Soils are young Andisols derived from postglacial volcanic ashes classified as Hapludands and Udivitrands (Ayasa et al. 2002). The island is mainly covered by three native and historically dominant plant communities, pure stands of the conifer *Austrocedrus chilensis* (D.Don) Florin & Boutleje (Cupressaceae), pure stands of the evergreen southern beech *Nothofagus dombeyi* Blume (Fagaceae), and shrublands co-dominated by *Lomatia hirsuta* (Lam.) Diels (Proteaceae) and *Maytenus boaria* Molina (Celastraceae). The understory plant composition varies by dominant overstory species, but it is generally dominated by the shrubs *Schinus patagonicus* (Phil.) I.M.Johnst. ex Cabrera (Anacardiaceae) and *Berberis darwinii* Hook (Berberidaceae), herbs, and graminoids. Wild boar colonized Isla Victoria in 1999 and currently are at high densities (>1 ha; M. N. Barrios-Garcia,

personal observation); however, there is no information on how boar disturbance varies across the island.

In 2008, we established exclosures and manipulated soil disturbance to test experimentally how foraging by boar alters the structure (plant community composition and biomass) and function (decomposition and nutrient cycles) of forested ecosystems. Based on observations that boar rooting patch size averaged 0.88m² and varied with forest type across the island, we established 10 circular exclosures (11 m²) in the three dominant plant communities—*Austrocedrus* forests, *Nothofagus* forests, and shrublands—in areas with no visible rooting activity. Exclosures were established in groups of 2 or 3 in several patches of each forest type; distance between exclosures varied from 100 m to 5 km apart. The exclosures were 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). Each exclosure was randomly divided into four quarters: in one quarter (2.75 m²) we experimentally manipulated boar activity by overturning the first 10 cm of the soil profile, while the other three quarters were left unmanipulated (Fig. 1). We conducted the experimental disturbance once in 2008 to tease apart the effect of soil disturbance

from other impacts that wild boar might have on the plant community or on ecosystem functioning. We established our boar-access plots adjacent to each enclosure. Four access plots (11 m², 0.5 m apart) were established in order to increase the likelihood that boar would disturb the area (Fig. 1). We conducted seasonal surveys of rooting disturbance by visually estimating the relative area (%) disturbed in the boar-access plots. Unless otherwise noted, data were collected during the austral summer of 2011.

To assess the effect of rooting treatments on plant communities, we harvested aboveground plant biomass at the end of the growing season (March 2011) in 0.5 × 0.5 m quadrats randomly placed within the three treatments (boar rooting, experimental rooting, and enclosure/non-rooting). Harvested plant material was oven-dried for approximately 48 hours at 60°C and weighed. We surveyed plant composition by identifying plant species and visually estimating the relative abundance (% cover) in the boar enclosure and surrounding access plots. Plant species were identified using Ezcurra and Brion (2005).

To investigate the effect of rooting treatments on decomposition rates, we established a leaf litter decomposition experiment in 2010. The upper side of each 10 × 10 cm decomposition bag was constructed with 2 layers of 0.8 mm polyester mesh and the lower side (facing the ground) was constructed of 0.2 mm window screen. Bags were stitched together on three sides with polyester thread and closed with stainless steel staples. Leaf litter used to fill decomposition bags was collected in nylon mesh collectors suspended beneath the crowns of *N. dombeyi* trees from November 2009 until February 2010. Leaf litter was collected bimonthly, air-dried, combined, homogenized and sorted to remove any non-litter material. We used *N. dombeyi* as a standard local substrate because we were interested in assessing the impact of rooting disturbance on decomposition, rather than differences due to litter quality. Decomposition bags contained 3 g of leaf litter and were placed in each of the three treatments (boar-access rooting, experimental rooting and boar-removal plots). We deployed the decomposition bags in February 2010 and retrieved and weighed them after 4 months (July 2010) and after 8 months (November 2010) of incubation. In total, we placed 162

decomposition bags (3 treatments × 27 enclosures × 2 collection dates). All data are shown on an ash-free oven-dry basis.

To measure the effects of rooting treatments on soil physical properties, nutrient dynamics, and nutrient availability we collected five soil samples in February 2011 (0–10 cm). Samples were collected from 6 enclosures of each of the three plant communities that had fresh rooting disturbance (<6 months), as in the remaining 4 enclosures rooting patches were older. Because we expected that the impact of rooting disturbance on soil properties might vary with time since disturbance, we also collected soil samples from patches that were rooted by boar 2 years earlier in 2008. Soil samples were stored in sealed plastic bags and transported immediately to the laboratory where they were sieved through a 2-mm mesh.

Soil temperature (0–10 cm) was taken in the field with a digital soil thermometer and soil moisture (0–12 cm) was measured with a TRIME-FM soil moisture device (Mesa Systems, USA). Soil compaction (0–15 cm) was assessed using an impact penetrometer (Synergy Resource Solutions, USA); we recorded the cumulative number of strikes required for each 5 cm depth increment (5, 10 and 15 cm) (Herrick et al. 2005). In the lab, air-dried soils were used to assess pH in water (1:2.5) (Page et al. 1982).

Wild boar rooting leads to mixing of the soil horizons, so we predicted soil turnover by rooting would increase potential soil carbon and nitrogen mineralization. We conducted a 40-day laboratory incubation to assess boar impacts on potential soil C and N mineralization. Approximately 100 g of sieved (2-mm) soil was brought up to field capacity and incubated in the dark at 25°C for 40 days. We extracted inorganic N (NO₃⁻, NH₄⁺) at the beginning (day 0) and after 40 days of incubation (day 40) with 2 M KCl. NO₃⁻ was determined by copperized Cd reduction and NH₄⁺-N by the Berthelot reaction (Keeney and Nelson 1982). Potential N mineralization rates were calculated as the difference between day 40 and day 0. We measured potential microbial activity, indicated by CO₂ accumulation, in 1.5-L glass jars that contained a 75 g soil sample (sieved to 2 mm, brought up to field capacity moisture), incubated in the dark at 25°C (Lerch et al. 1992). At days 7, 16 and 40, CO₂

was determined using vial traps of 0.2 M NaOH titrated with HCl (Lerch et al. 1992). Microbial respiration was estimated as cumulative CO₂ evolution during the incubation period.

Total organic C and total N were analyzed on air-dried samples sieved through a 0.5-mm mesh using a NC Soil Analyzer Flash EA 1112 at 900°C combustion (Thermo Electron, USA). Extractable P was assessed with air-dried soil samples in 0.5 M NaHCO₃ (1:20, soil:solution ratio) by the molybdate ascorbic acid method.

We used a nested ANOVA to test for the effects of fence, rooting[fence] (boar rooting, experimental rooting, and enclosure/no rooting) and forest type (*Austrocedrus* forest, *Nothofagus* forest, and shrubland) on plant biomass and functional groups, and on decomposition rates. When our models were significant we used Tukey-Kramer post-hoc tests to compare means. We analyzed plant composition changes using data from all plots (enclosure and 4 open plots) with PERMANOVA, using the Bray-Curtis dissimilarity matrix on log-transformed abundance data and percent rooting as a co-variable (Primer-E). To analyze the effect of rooting (boar rooting <month, boar rooting 2 years, experimental rooting, and enclosure/no rooting) and forest type (*Austrocedrus* forest, *Nothofagus* forest, and shrubland) on soil properties we used separate two-way ANOVAs. When necessary, data were log-transformed to meet normality assumptions; however, figures show untransformed mean values. Data from 27 of the enclosures were used, as three unfenced areas in shrubland had no rooting activity after the establishment of the experiment in 2008 (all data points were excluded: boar rooting, experimental rooting, and no rooting). All statistical analyses were conducted using JMP Pro 10 statistical software with alpha set a priori as $\alpha < 0.05$ (SAS Institute, Pacific Grove, CA, USA, 2001).

RESULTS

We analyzed the effects of wild boar rooting and ecosystem-type on our response variables independently because there were no significant interaction terms between boar rooting and forest type (see Appendix: Table A1; Underwood 1996). Thus our results will focus on the effects of boar rooting vs. ecosystem-type on ecosystem struc-

ture and function.

Rooting by boar reduced aboveground plant biomass 3.8-fold relative to the enclosure and 2.3-fold relative to the experimentally rooted areas (nested ANOVA, $P < 0.001$, $F_{8,80} = 8.63$; Figs. 1 and 2A; Appendix: Table A1), and there was a significant effect of ecosystem-type: plant biomass was ~1.5-fold greater in *Austrocedrus* forests and shrublands compared to *Nothofagus* forests (Appendix: Table A1). Furthermore, plant composition differed significantly among rooting treatments (PERMANOVA, pseudo $F = 1.94$, $P = 0.014$) and ecosystem-type (PERMANOVA, pseudo $F = 40.41$, $P < 0.001$): rooting disturbance reduced grass and herb cover by 1.3-fold and 1.2-fold, respectively, relative to the enclosure (nested ANOVA, $P < 0.001$, $F_{8,149} = 58.72$; $P < 0.001$, $F_{8,149} = 8.55$, respectively; Fig. 2). Tree cover was similar across ecosystems, but shrub cover was greater in *Austrocedrus* forest, intermediate in *Nothofagus* forest, and least in shrubland ($25.5 \pm 1.88\%$, $20.18 \pm 1.79\%$, and $19.76 \pm 2.46\%$, respectively); herb cover was ~2-fold greater in shrubland than in *Nothofagus* and *Austrocedrus* forest ($29.12 \pm 1.87\%$, $14.38 \pm 1.27\%$, and $13.8 \pm 1.42\%$, respectively) and grass cover was ~11-fold greater in shrubland and *Austrocedrus* forest than in *Nothofagus* forest ($44.96 \pm 2.99\%$, $43.72 \pm 2.81\%$, and $3.72 \pm 1.02\%$, respectively).

Leaf litter lost approximately 25% of its mass after 8 months of decomposition. Decomposition was 5% slower in plots where boar had rooted than in experimentally rooted and enclosure plots (nested ANOVA, $P = 0.012$, $F_{8,80} = 2.67$; Fig. 3, Appendix: Table A1). By contrast, decomposition did not vary among forest types ($P > 0.25$; Fig. 3, Appendix: Table A1).

Belowground properties showed minimal effects of rooting disturbance. As expected, rooting by boar decreased soil compaction (0–5 cm) by 5% relative to experimental rooting and enclosure plots (two-way ANOVA, $P < 0.001$, $F_{3,71} = 9.42$; Fig. 4), and there was an ecosystem-type effect, indicating greater soil compaction in shrubland than in *Austrocedrus* and *Nothofagus* forest (two-way ANOVA, $P < 0.001$, $F_{2,71} = 12.02$; Fig. 4). Interestingly, we were unable to detect an effect of boar rooting on the other soil variables we measured (Appendix: Tables A2 and A3), but they did vary among forest types (Appendix: Table A4). Specifically, soil temperature and

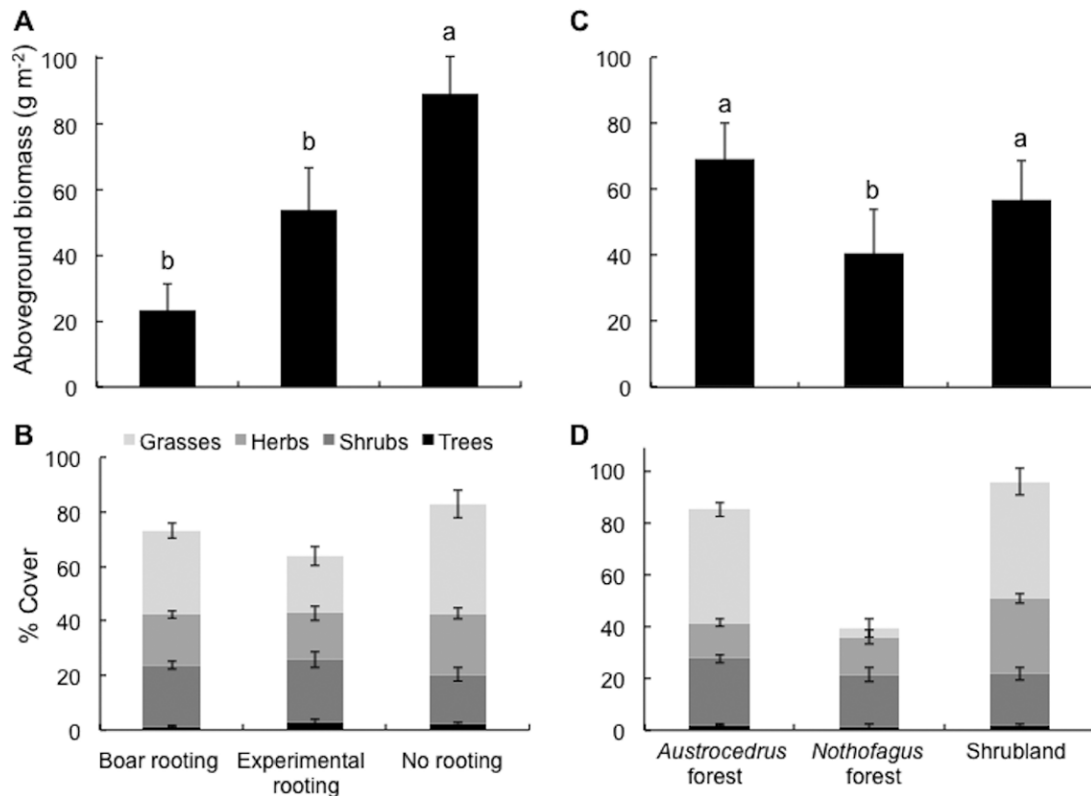


Fig. 2. Wild boar rooting decreases aboveground plant biomass 3.8× relative to areas where they are excluded (A, mean ± SE, letters indicate significant differences among treatments) and alters plant community composition by decreasing both grass and herb functional groups (B). Forest types significantly differ in terms of aboveground biomass and plant species composition, *Nothofagus* forest has ~1.5-fold less biomass relative to *Austrocedrus* forest and shrubland (C), where grasses are 12-fold less abundant and forbs 2-fold less abundant (D). Different lowercase letters indicate significant differences at $P < 0.05$.

moisture were greater in shrubland ($21.5 \pm 0.9^\circ\text{C}$, $13.8 \pm 1.2\%$) than in *Austrocedrus* ($16.2 \pm 0.3^\circ\text{C}$, $6.5 \pm 0.3\%$) and *Nothofagus* ($15.4 \pm 0.3^\circ\text{C}$, $8.2 \pm 0.6\%$) forest (two-way ANOVA, $P_{\text{temp}} < 0.001$, $F_{2,71} = 31.21$ and $P_{\text{mois}} < 0.001$, $F_{2,71} = 28.59$; Appendix: Table A4). Similarly, pH was highest in *Austrocedrus* forest (6.43), intermediate in *Nothofagus* forest (6.28), and lowest in shrubland (6.05, $P < 0.001$, $F_{2,71} = 13.85$); N mineralization was 2-fold higher in *Nothofagus* forest than in *Austrocedrus* forest and shrubland ($P < 0.001$, $F_{2,71} = 50.65$); while soil respiration was 2.3-fold higher in *Nothofagus* forest than in shrubland and 1.2-fold higher in *Nothofagus* forest than in *Austrocedrus* forest ($P < 0.001$, $F_{2,71} = 81.32$). Nutrient availability data showed that total C content was 30% greater in *Austrocedrus* and *Nothofagus* forest than in shrubland ($P < 0.001$,

$F_{2,71} = 17.57$). Total N content did not differ among ecosystem-types, while extractable P was higher in *Nothofagus* forest ($11.3 \mu\text{g P g}^{-1}$ soil), intermediate in *Austrocedrus* forest ($7.50 \mu\text{g P g}^{-1}$ soil), and lower in shrubland ($4.51 \mu\text{g P g}^{-1}$ soil) ($P < 0.001$, $F_{2,71} = 17.72$; Appendix: Table A4).

DISCUSSION

Although wild boar were introduced relatively recently, their activity has shifted the abundance and community composition in Patagonia forests. Boar rooting reduced plant biomass 60% relative to unrooted areas. Interestingly and unexpectedly, there was no interaction between boar activity and forest type. Also, in spite of their significant soil disturbance, boar had minimal impacts on the soil system after three

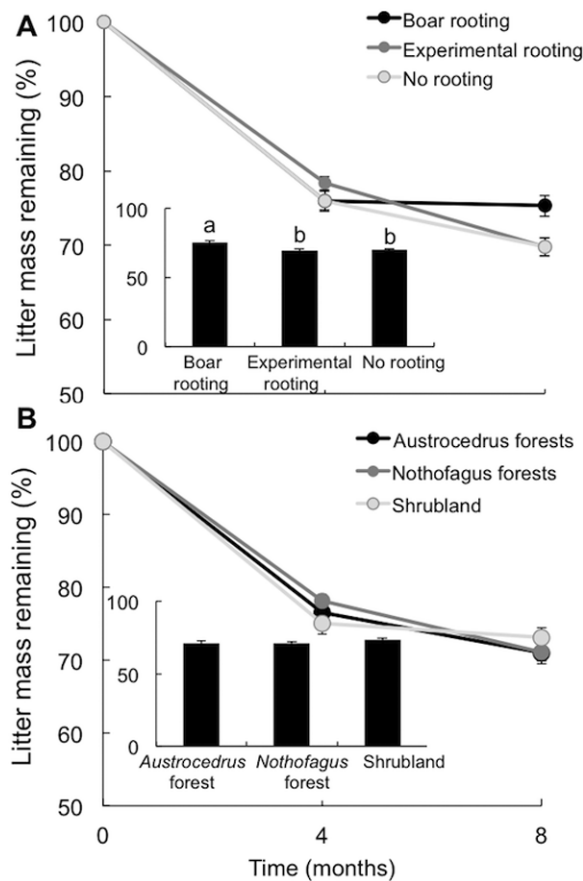


Fig. 3. Litter decomposition rates (% mass loss) were 5% lower in non-rooted areas than in rooted areas after 8 month (A, mean \pm SE). However, there were no differences in decomposition rates among forest types (B). Histograms show mean mass remaining (%) after 8 months in each of the treatments. Different lowercase letters indicate significant differences at $P < 0.05$.

years of exclusion. However, nutrient cycling did vary by forest type. Our results indicate that, in these ecosystems after 12 years of introduction, boar rooting had a larger impact aboveground than belowground, indicating disparate above- and belowground processes.

Similarly to other studies, we found that boar reduced plant biomass by 60% and grasses and herbs were the most impacted by disturbance (Bratton 1974, 1975, Singer et al. 1984, Kotanen 1995, Hone 2002, Tierney and Cushman 2006). For example, introduced wild boar herbivory in grey beech forests of the USA reduced understorey plant cover by 90% (Bratton 1975), while boar

disturbance in coastal California reduced plant richness by 29% (Cushman et al. 2004). Here, we examined the impact of boar activity on plant biomass and composition in three ecosystems. Because we found a strong effect of rooting on plant biomass and no interaction with forest type, we can argue that boar activity has a similar impact across ecosystems despite large differences in composition and structure. While the lack of a forest type by rooting interaction surprised us, we think this result can be explained by the boar's diet. Boar are generalist feeders, which has allowed them to establish populations almost anywhere they are introduced (Ballari and Barrios-Garcia 2014), indicating a great ability to find resources in a variety of ecosystems.

Belowground mammalian herbivory can stimulate decomposition (Sherrod and Seastedt 2001); however, we found that boar activity decreased decomposition. Microclimate, litter quality, and the soil community are all drivers of decomposition at the local scale (Swift et al. 1979, Seastedt 1984), and we can account for two of these drivers in our study. Rooting in our study had no effect on microclimate or on soil microbial activity. Soil moisture, temperature, and even microbial activity (N mineralization and soil respiration) were similar across our treatments. To control for litter quality differences, we used a standard litter substrate at each of our sites. While we did not assess changes in the soil community, we suspect wild boar activity might be slowing decomposition rates by their foraging on macrofauna (Bradford et al. 2002, Hättenschwiler et al. 2005, Bardgett and Wardle 2010). Wild boar can reduce litter-dwelling animals up to 10-fold, suggesting their foraging may be altering fractionation of litter material by macrofauna, the first step of litter decomposition (Vtorov 1993). Over the 8-month decomposition experiment, we observed the initial phase of decomposition where macrofauna play a large role in fragmentation, thus lending support for our hypothesis. While the difference in decomposition rates between rooted and exclosure plots was small, these rates will likely compound over time and thus might alter the soil carbon cycle.

Surprisingly we found minimal effects of boar rooting on soil properties, but soil properties did vary by forest type. We hypothesized that bioturbation of soil by boar would decrease soil

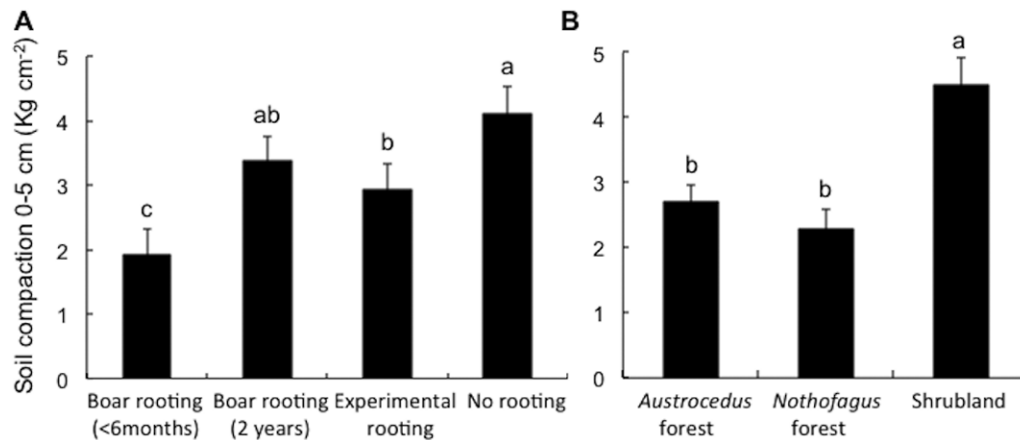


Fig. 4. Rooting by wild boar decreases soil compaction by 2× relative to unrooted areas (A). Soil compaction is ~1.8× greater in shrubland than in *Austrocedus* and *Nothofagus* forest (B). Different lowercase letters indicate significant differences at $P < 0.05$.

compaction, increase soil temperature, decrease soil moisture, and increase nutrient availability and cycling because rooting incorporates organic material into the mineral soil (Singer et al. 1984). In spite of significant soil disturbance—up to 33% of the area rooted every winter—boar rooting in our system reduced only soil compaction. Our findings, while surprising, are consistent with previous studies that showed idiosyncratic effects of rooting on soil properties and processes (Singer et al. 1984, Groot Bruinderink and Hazebroek 1996, Moody and Jones 2000, Cushman et al. 2004, Mohr et al. 2005, Tierney and Cushman 2006, Siemann et al. 2009). Two mechanisms might explain the absence of response of soil properties to rooting disturbance: soil resilience and the temporal scale. Soils in northwestern Patagonia are derived from volcanic ash with high capacity to stabilize soil organic matter, buffer pH, and retain P and water, which makes them highly resistant to nutrient loss and disturbance (Diehl et al. 2003, Alauzis et al. 2004). Time might also play a role.

Soils can be well buffered to short-term disturbances. Thus, the impacts of rooting might increase with more rooting events over time (Bardgett et al. 2005). Many studies show effects of disturbance by mammals on belowground processes that are detectable within months of the disturbance event (Tardiff and Stanford 1998, Reichman and Seabloom 2002). These changes mostly result from altered abiotic conditions

(temperature and moisture). However, belowground processes are also influenced by the quality of resource inputs (Bardgett et al. 2005). Therefore, we cannot rule out the possibility that long-term changes in plant community composition will exert effects on soil biological properties.

The experimentally rooted plots showed mixed responses as plant biomass was reduced by 30 %, but no effects were detected on soil properties or decomposition rates. We set up the experimentally rooted plots to tease apart the effects of belowground mammalian herbivory and soil disturbance. However, the experimental rooting was conducted only once in 2008, 3 years prior to data collection. The time lapse of 3 years allowed some plant revegetation (although there was still less plant growth than in undisturbed [exclosure] conditions) and possibly the recovery of soil properties and decomposition rates. Similarly, previous work by Tierney and Cushman (2006) found no significant variation in soil nutrient pools and cycling with time since disturbance by boar in coastal California (2, 14, 26 and 60 months). The results of our experimentally rooted plots lend support to our hypothesis that the soils at our sites resist short-term soil disturbances. It is possible, especially given the plant community changes, that after many years of repeated rooting events the soils at our site will alter nutrient pools and fluxes at our site.

CONCLUSION

Mammalian herbivores, especially those foraging for belowground plant material, can structure ecosystems (Andersen 1987, Whitford and Kay 1999, Gutiérrez and Jones 2006). However, this impact may have negative effects if invasive herbivores are introduced into ecosystems where belowground mammalian foraging was not originally present. Previous studies have either explored the role of native belowground herbivory (Tardiff and Stanford 1998, Reichman and Seabloom 2002, Canals et al. 2003) or the influence of invasive mammalian herbivores (Wardle et al. 2001, Husheer et al. 2003, Côté et al. 2004) on ecosystem processes, while ours provides new insights on how belowground herbivory by an invasive mammal influences ecosystems. Our results show that, even after a few years of introduction, belowground foraging by invasive wild boar can disrupt ecosystem structure and processes by decreasing plant primary productivity, decomposition rates, and organic matter turnover. We were surprised that there was minimal effect of rooting on soil properties and the effect of rooting was the same in each forest type. Although our results show disparate responses of above- and belowground processes to introduced wild boar activity, belowground impacts may take longer to develop in these ecosystems and could potentially accumulate over time to influence ecosystem trajectory (Bardgett et al. 2005). For example, Lacki and Lancia (1986) showed that rooting by wild boar influenced tree growth in Great Smoky Mountains National Park. Finally, our study provides new evidence on how invasive wild boar populations can alter ecosystem functioning.

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LITERATURE CITED

- Alauzis, M. V., M. J. Mazzarino, E. Raffaele, and L. Roselli. 2004. Wildfires in NW Patagonia: long-term effects on a *Nothofagus* forest soil. *Forest Ecology and Management* 192:131–142.
- Andersen, D. C. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. *Quarterly Review of Biology* 62:261–286.
- Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications* 13:1325–1337.
- Ayesa, J. A., C. R. Lopez, D. E. Bran, F. J. Umana, and P. A. Lagorio. 2002. Cartografía biofísica de la Patagonia Norte. INTA Estacion Experimental Agropecuaria Bariloche, PAN, PRODESAR.
- Ballari, S. A. and M. N. Barrios-Garcia. 2014. A review of wild boar (*Sus scrofa*) diet and factors affecting food selection in the native and introduced ranges. *Mammal Review* 44:124–134.
- Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt. 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution* 20:634–641.
- Bardgett, R. D. and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268.
- Bardgett, R. D. and D. A. Wardle. 2010. Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford University Press New York, New York, USA.
- Bradford, M., T. H. Jones, R. D. Bardgett, H. I. J. Black, B. Boag, M. Bonkowski, R. Cook, T. Eggers, A. Gange, and S. J. Grayston. 2002. Impacts of soil faunal community composition on model grassland ecosystems. *Science* 298:615–618.
- Bratton, S. P. 1974. Effect of European wild boar (*Sus scrofa*) on high-elevation vernal flora in Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical 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.
- Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147.
- Cushman, J. H., T. A. Tierney, and J. M. Hinds. 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. *Ecological Applications* 14:1746–1756.
- Diehl, P., M. Mazzarino, F. Funes, S. Fontenla, M. Gobbi, and J. Ferrari. 2003. Nutrient conservation

- strategies in native Andean-Patagonian forests. *Journal of Vegetation Science* 14:63–70.
- Eldridge, D. J. and A. Mensinga. 2007. Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland. *Soil Biology and Biochemistry* 39:1055–1065.
- Ezcurra, C. and C. Brion. 2005. Plantas del Nahuel Huapi: Catálogo de la Flora Vascular del Parque Nacional Nahuel Huapi, Argentina. Universidad Nacional del Comahue San Carlos de Bariloche, Argentina.
- Fukami, T., D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. R. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, and W. M. Williamson. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* 9:1299–1307.
- Groot Bruinderink, G. and E. Hazebroek. 1996. Wild boar (*Sus scrofa scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. *Forest Ecology and Management* 88:71–80.
- Gutiérrez, J. L. and C. G. Jones. 2006. Physical ecosystem engineers as agents of biogeochemical heterogeneity. *BioScience* 56:227–236.
- Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 36:191–218.
- Herrick, J. E., J. W. V. Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. Volume I: Quick Start. Volume II: Design, supplementary methods and interpretation. USDA ARS, Jornada Experimental Range.
- Hone, J. 2002. Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* 105:231–242.
- Hooper, D. U., D. E. Bignell, V. K. Brown, L. Brussard, J. Mark Dangerfield, D. H. Wall, D. A. Wardle, D. C. Coleman, K. E. Giller, and P. Lavelle. 2000. Interactions between aboveground and below-ground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience* 50:1049–1061.
- Huntly, N. and O. Reichman. 1994. Effects of subterranean mammalian herbivores on vegetation. *Journal of Mammalogy* 85:852–859.
- Husheer, S. W., D. A. Coomes, and A. W. Robertson. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. *Forest Ecology and Management* 181:99–117.
- Keeney, D. R., and D. W. Nelson. 1982. Nitrogen-inorganic forms. Pages 643–698 in A. L. Page, R. H. Miller, and D. R. Keeney, editors. *Methods of soil analysis, part 2*. Second edition. Series Agronomy No. 9. ASA, SSSA, Madison, Wisconsin, USA.
- Kotanen, P. M. 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. *Ecography* 18:190–199.
- Lacki, M. J. and R. A. Lancia. 1986. Effects of wild pigs on beech growth in Great Smoky Mountains National Park. *Journal of Wildlife Management* 50:655–659.
- Lerch, R., K. Barbarick, L. Sommers, and D. Westfall. 1992. Sewage sludge proteins as labile carbon and nitrogen sources. *Soil Science Society of America Journal* 56:1470–1476.
- Li, X., M. C. Fisk, T. J. Fahey, and P. J. Bohlen. 2002. Influence of earthworm invasion on soil microbial biomass and activity in a northern hardwood forest. *Soil Biology and Biochemistry* 34:1929–1937.
- Mohr, D., L. W. Cohnstaedt, and W. Topp. 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biology & Biochemistry* 37:693–700.
- Moody, A. and J. A. Jones. 2000. Soil response to canopy position and feral pig disturbance beneath *Quercus agrifolia* on Santa Cruz Island, California. *Applied Soil Ecology* 14:269–281.
- Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467–480.
- Reichman, O. and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution* 17:44–49.
- Seastedt, T. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29:25–46.
- Sherrod, S. K. and T. R. Seastedt. 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry* 55:195–218.
- Siemann, E., J. A. Carrillo, C. A. Gabler, R. Zipp, and W. E. Rogers. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management* 258:546–553.
- Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. *Journal of Wildlife Management* 48:464–473.
- Sirotnak, J. M. and N. J. Huntly. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81:78–87.
- Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. *Decomposition in terrestrial ecosystems*. University of California Press.
- Tardiff, S. E. and J. A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology* 79:2219–2228.

- Tierney, T. A. and J. H. Cushman. 2006. Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. *Biological Invasions* 8:1073–1089.
- Underwood, A. J. 1996. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.
- Vtorov, I. P. 1993. Feral pig removal: effects on soil microarthropods in a Hawaiian rain forest. *Journal of Wildlife Management* 57:875–880.
- Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: Above-ground and belowground consequences. *Ecological Monographs* 71:587–614.
- Whitford, W. G. and F. R. Kay. 1999. Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* 41:203–230.

SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Results from nested ANOVAs examining the effects of fence, rooting[fence] (boar-rooting, experimental rooting, and no-rooting), plant communities (*Austrocedrus* forest, *Nothofagus* forest, and shrublands), and their interaction on aboveground biomass, tree cover, shrub cover, herb cover, grass cover, and litter decomposition (error df for aboveground biomass and litter decomposition 72, error df for plant function groups 141). Bold values are significant at $P < 0.05$.

Source	df	F-ratio	P
Aboveground biomass (g/m ²)			
Model	8	8.63	<0.001
Fence	1	19.69	<0.001
Rooting[fence]	1	8.60	0.004
Community	2	14.68	<0.001
Community × fence	2	3.28	0.043
Community × rooting[fence]	2	1.33	0.27
Tree cover (%)			
Model	8	0.83	0.572
Fence	1	3.26	0.073
Rooting[fence]	1	0.11	0.740
Community	2	0.23	0.794
Community × fence	2	0.12	0.886
Community × rooting[fence]	2	1.23	0.295
Shrub cover (%)			
Model	8	2.67	0.009
Fence	1	0.45	0.505
Rooting[fence]	1	0.66	0.416
Community	2	6.91	0.001
Community × fence	2	0.20	0.816
Community × rooting[fence]	2	2.49	0.086
Herb cover (%)			
Model	8	8.55	<0.001
Fence	1	0.20	0.655
Rooting[fence]	1	8.85	0.003
Community	2	28.10	<0.001
Community × fence	2	0.03	0.968
Community × rooting[fence]	2	0.76	0.468
Grass cover (%)			
Model	8	58.72	<0.001
Fence	1	0.19	0.660
Rooting[fence]	1	16.37	<0.001
Community	2	212.01	<0.001
Community × fence	2	0.63	0.532
Community × rooting[fence]	2	0.47	0.627
Litter decomposition(% mass remaining)			
Model	8	2.67	0.012
Fence	1	13.44	0.001
Rooting[fence]	1	0.01	0.967
Community	2	1.43	0.246
Community × fence	2	3.49	0.036
Community × rooting[fence]	2	0.05	0.952

Table A2. Results from a two-way ANOVA examining the effects of rooting (boar-rooting <6 months, boar-rooting 2 years, experimental rooting, and no-rooting), plant communities (*Austrocedrus* forest, *Nothofagus* forest, and shrublands), and their interaction on soil properties (error df = 60). Bold values are significant at $P < 0.05$.

Source	df	F-ratio	P
Soil temperature (0–10 cm)			
Model	11	5.73	<0.001
Rooting	3	0.08	0.972
Community	2	31.21	<0.001
Interaction	6	0.07	0.999
Volumetric soil moisture (0–10 cm)			
Model	11	5.65	<0.001
Rooting	3	0.51	0.677
Community	2	28.59	<0.001
Interaction	6	0.61	0.718
Soil compaction (5 cm)			
Model	11	5.27	<0.001
Rooting	3	9.422	<0.001
Community	2	12.02	<0.001
Interaction	6	0.79	0.5773
pH			
Model	11	2.87	<0.001
Rooting	3	0.65	0.585
Community	2	13.85	<0.001
Interaction	6	0.29	0.937
N mineralization (μg N/kg soil)			
Model	11	9.73	<0.001
Rooting	3	0.80	0.501
Community	2	50.65	<0.001
Interaction	6	0.55	0.764
Soil respiration (CO ₂ mg/kg soil)			
Model	11	15.63	<0.001
Rooting	3	0.29	0.829
Community	2	81.32	<0.001
Interaction	6	1.13	0.357
Total C (%)			
Model	11	3.70	<0.001
Rooting	3	0.54	0.657
Community	2	17.57	<0.001
Interaction	6	0.64	0.697
Total N (%)			
Model	11	0.75	0.690
Rooting	3	0.28	0.836
Community	2	2.38	0.102
Interaction	6	0.42	0.862
Extractable P (μg/g)			
Model	11	3.74	<0.001
Rooting	3	0.90	0.962
Community	2	17.72	<0.001
Interaction	6	0.88	0.514

Table A3. Soil property means (SE) by rooting treatments ($P > 0.05$), indicating a lack of significant differences.

Soil property	Boar rooting fresh (<6 months)	Boar rooting old (2 years)	Experimental rooting (2 years)	No rooting
Temperature (°C)	17.74 (1.01)	17.58 (0.96)	17.35 (0.81)	17.25 (0.79)
Volumetric soil moisture (%)	10.39 (1.59)	9.30 (1.05)	9.14 (1.16)	8.70 (1.15)
pH	6.28 (0.09)	6.30 (0.06)	6.26 (0.07)	6.18 (0.06)
N mineralization (µg N/kg soil)	55770.59 (7629.32)	56488.24 (6882.49)	62111.76 (6716.62)	56264.71 (6032.22)
Soil respiration (CO ₂ mg/kg soil)	5546.99 (590.92)	5006.17 (535.56)	5057.34 (384.58)	5160.14 (603.31)
C (%)	10.34 (0.73)	9.45 (0.62)	9.40 (0.49)	9.77 (0.71)
N (%)	0.59 (0.04)	0.56 (0.03)	0.55 (0.03)	0.58 (0.04)
Extractable P (µg/g)	8.92 (1.62)	7.92 (1.14)	7.03 (0.61)	7.98 (1.37)

Table A4. Soil property means (SE) by ecosystem type. Different superscript letters indicate significant differences at $P < 0.05$.

Soil property	<i>Austrocedrus</i> forest	<i>Nothofagus</i> forest	Shrubland
Temperature (°C)	16.22 ^B (0.32)	15.39 ^B (0.29)	21.51 ^A (0.90)
Volumetric soil moisture (%)	6.46 ^B (0.29)	8.18 ^B (0.63)	13.79 ^A (1.22)
pH	6.43 ^A (0.05)	6.28 ^A (0.06)	6.03 ^B (0.03)
N mineralization (µg N/kg soil)	44050.00 ^B (2948.58)	87270.83 ^A (4551.40)	38455.00 ^B (2427.47)
Soil respiration t40 (CO ₂ mg/kg soil)	5464.98 ^B (151.16)	6891.22 ^A (363.13)	2939.59 ^C (145.39)
C (%)	11.00 ^A (0.55)	10.36 ^A (0.45)	7.48 ^B (0.29)
N (%)	0.61 (0.03)	0.58 (0.03)	0.52 (0.03)
Extractable P (µg/g)	7.50 ^B (0.63)	11.3 ^A (1.23)	4.51 ^C (0.60)