

# Litter microbial and soil faunal communities stimulated in the wake of a volcanic eruption in a semi-arid woodland in Patagonia, Argentina

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## Summary

1. Large-scale disturbances can be important components of the temporal landscape of natural ecosystems, but generalities regarding ecosystem impacts are difficult due to their infrequent and unpredictable nature. Volcanic eruptions figure as one of the most prominent of these natural disturbances, but the effects on microbes and ground-dwelling arthropods, which modulate carbon and nutrient turnover, are relatively unknown.

2. We evaluated the effects of the 2011 Puyehue-Cordón Caulle eruption in Patagonia, Argentina, on the litter and soil microbial and faunal communities in natural and afforested semi-arid ecosystems located 70 km west of the epicentre of the eruption. We hypothesized that volcanic ash deposition would strongly reduce soil faunal and microbial communities due to insecticidal effects of ash on arthropods, with a concomitant reduction in ecosystem processes.

3. Our objective was to quantify the impact of the volcanic eruption by comparing pre- and post-eruption time points in the same study site, with nearly identical field methodology. We measured environmental variables of soil and litter moisture, pH, microbial biomass, and soil and litter microbial enzymatic activity. We evaluated ground-dwelling arthropods and nematodes using pitfall traps and soil extraction, respectively. Additionally, a parallel, controlled-condition experiment of simulated ash deposition was conducted to evaluate ash effects on litter decomposition and enzymatic activity.

4. In the field, post-eruption soils had lower soil water content, pH and soil organic matter. Additionally, nematode abundance and soil microbial enzyme activity were significantly reduced. In contrast, ground-dwelling arthropods and litter enzymatic activity increased significantly. Finally, with simulated ash deposition, litter decomposition increased fourfold for native litter decomposition.

5. Large-scale disturbances may play a key role in biogeochemical cycling in affected natural ecosystems, but not necessarily due to their catastrophic effects. In contrast to our original predictions, we observed a marked stimulation of biotic activity and carbon turnover in the aftermath of the Puyehue volcanic eruption, which demonstrates that the biotic component of these ecosystems has a substantial capacity to respond to these disturbances in short time frames. These results can contribute to placing the role of these large-scale infrequent disturbances in a more robust ecological context.

**Key-words:** ash deposition, biogeochemical cycles, carbon, ground-dwelling arthropods, large-scale disturbance, litter decomposition, nematodes, soil fauna, volcanic eruption

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## Introduction

Natural disturbances, which vary in intensity, magnitude and frequency, form a part of the temporal landscape of many ecosystems, affecting population dynamics and the variability of ecosystem processes (Paine, Tegner & Johnson 1998; Motzkin *et al.* 1999; Fraterrigo & Rusak 2008). These disturbances include such varied events as hurricanes, volcanic eruptions, fires, frosts and population explosions of pests and pathogens. Disturbances at the landscape scale will be reflected in ecosystem processes as a function of the underlying characteristics of the ecosystem and the interaction with abiotic factors. Nevertheless, due to their unpredictable and infrequent nature, it is a continuing challenge to understand how these disturbances affect the trajectories of succession and ecosystem development (Chapin, Matson & Mooney 2002). Specifically, biogeochemical cycles can be markedly affected by large-scale disturbances, causing changes in nutrient pools and turnover, above- and below-ground biomass, and soil faunal and microbial communities.

In spite of their potential importance in affecting ecosystem structure and function, large-scale disturbances have been explored much less frequently than, periodic small-scale disturbances (Turner, Dale & Everham 1997). The inability to replicate these events in a reasonable time frame and the absence of a pre-event control are other difficulties that complicate the accurate appraisal of these events on ecosystem functioning. Generally, the main focus of the response to large-scale disturbances in terrestrial ecosystems is on trajectories of succession in the plant community (Antos & Zobel 2005), and as such, there is little information on how these large-scale disturbances may affect below-ground communities, which are key links to biogeochemical cycling (Wardle *et al.* 2004). In particular, insects and other arthropods appear to be quite vulnerable to intense fire or volcanic eruptions, with severely reduced populations in the wake of these events (Schowalter 2012; Elizalde 2014). In some instances, however, disturbances can result in insect outbreaks due to stress on other biotic components, such as drought-induced mortality of vegetation (Raffa *et al.* 2008; Schowalter 2012). A more complete understanding of the biotic responses of key players in biogeochemical cycling is important to interpret and predict the effects of large-scale disturbances on ecosystem functioning (Turner, Dale & Everham 1997).

Volcanic eruptions correspond to one of the largest natural disturbances and their effects in ecosystems are varied and complex (Del Moral & Grishin 1999; Self 2006). These effects can range from global effects on climate forcing (Robock 2000) to wide-ranging ecological impacts in terrestrial and aquatic ecosystems (Del Moral & Jones 2002; Flueck & Smith-Flueck 2013; Modenutti *et al.* 2013; Wolinski *et al.* 2013). Distance from the eruption site (Antos & Zobel 2005), the type of material (Del Moral & Jones 2002) and species characteristics are all important factors in determining ecosystem responses, but

quantitative ecological information prior to volcanic eruptions that would allow for direct comparison is very rare.

The massive pyroclastic eruption of Mount Saint Helens, located in the Pacific North-west region of the United States, in May 1980 has become the most studied volcanic eruption in the world (Dale, Crisafulli & Swanson 2005). This event has provided one of the best opportunities to explore the ecological responses in terrestrial ecosystems to this kind of disturbance. Numerous studies have evaluated floristic changes in the years following the eruption (e.g. Del Moral & Wood 1988; Morris & Wood 1989; Antos & Zobel 2005). Two major conclusions from long-term studies of plant succession are that the rate of recovery of the plant community is largely due to the number of individuals surviving the disturbance (Del Moral & Wood 1988): and that successional trajectories, and particularly the reinvasion of lupine species, are affected by plant–herbivore interactions, with insect herbivory inhibiting the spread of lupines into moderately impacted areas (Fagan, Bishop & Schade 2004; Fagan *et al.* 2005).

Long-term data from the Mt. St. Helens site demonstrated that soil C and N pools increased in the years post-eruption but that within 15 years, most nutrient pools had stabilized (Halvorson, Smith & Franz 1991; Halvorson & Smith 2009). Other aspects of ecosystem functioning, including the impacts on soil faunal communities and soil processes, were much less studied (Edmonds & Erickson 1994; Erickson & Edmonds 1994) and did not benefit from pre-eruption population estimates or baseline carbon and nutrient cycling. Nevertheless, arthropods might be key players in affecting biogeochemical cycling after this type of large-scale disturbance because of their capacity for widespread dispersal, and their roles in community assembly processes and soil formation (Edwards 1986). Volcanic eruptions can cause mortality and affect the habitat of arthropods, changing food sources, shelter and microclimate conditions (Del Moral & Grishin 1999; Elizalde 2014), and reduce insect herbivory and the strength of plant–pollinator interactions (Bishop *et al.* 2005; Chaneton *et al.* 2014) but it is not clear how soil fauna that are linked to carbon and nutrient turnover might be affected. Given this, a broader understanding of the effects of natural disturbances on soil biota is important for evaluating the impacts of volcanic eruptions on ecosystem functioning.

## THE 2011 ERUPTION OF PUYEHUE-CORDÓN CAULLE VOLCANO

As part of the chain of volcanoes that form the Pacific ring of fire, volcanic activity has been prominent in the Patagonia region from the initial uplift which created the Andes mountain chain, and eruptions often occur with little warning (Castro & Dingwell 2009). Currently, there are a number of active volcanoes in the Patagonian Andes, with a sustained occurrence of pyroclastic eruptions documented during the Holocene (Singer *et al.* 2008; Stern 2008). As a consequence, ash deposition in surrounding

terrestrial and lacustrine ecosystems is a recurrent disturbance and forms a part of the parent material for soil genesis (Cremona, Ferrari & López 2011) and lake sediments (Modenutti *et al.* 2013).

The massive eruption of the Puyehue-Cordón Caulle (CVPCC) (40°35'25"S 72°7'2"W) in June of 2011 affected a considerable part of the Patagonian region. The Puyehue-Cordón Caulle volcanic complex consists of two broad shield volcanoes which have been active in two recent eruptions affecting the region in 1921 and 1960 (Singer *et al.* 2008). The Puyehue volcano expelled large amounts of pyroclastic material of variable size and texture into the atmosphere on 4 June 2011 that, due to the predominance of westerly winds, were deposited in an eastern trajectory towards the Atlantic Coast (Cremona, Ferrari & López 2011; Gaitán *et al.* 2011). Several hundred million tons of volcanic tephra were dispersed over *c.* 25000 km<sup>2</sup>, along a west-to-east gradient (Gaitán *et al.* 2011) of the Argentine provinces of Neuquén, Chubut and Río Negro and reaching areas of southern Buenos Aires (Bermúdez & Delpino 2011). There was a directional shift in ash-grain size and thickness of tephra deposits (i.e. a proxy for disturbance intensity, *sensu* Pickett & White 1985). The severity of the event impact on plant mortality and depth of ash deposition varied with distance to the eruption site (Bermúdez & Delpino 2011).

The eruption of the Puyehue-Cordón Caulle provides the opportunity to study the responses of native and modified ecosystems in the context of a large-scale natural disturbance. Our specific objective was to assess the changes induced by the volcanic eruption in the abundance, composition and function of soil microbial and faunal communities in a zone impacted by ash deposition in a semi-arid site in Patagonia, Argentina.

We hypothesized that in the aftermath of this volcanic eruption, the abundance and community composition of soil fauna would be negatively affected in multiple ways. Direct assessment of the immediate effects of volcanic ash in natural populations of arthropods in the wake of the Mt. St. Helens eruption demonstrated a level of damage to arthropods that was equivalent to the application of broad spectrum insecticide (Edwards & Schwartz 1981), with extremely high mortality near the epicentre of the eruption for some groups such as Coleoptera (Parmenter *et al.* 2005). Insecticidal effects on herbivorous insects were also observed in the aftermath of the eruption of Puyehue (Chaneton *et al.* 2014), which was attributed to both dehydration and mechanical abrasion of cuticles. Given this previous evidence, we predicted that ash deposition would reduce soil arthropod abundance. In addition, we predicted that abiotic impacts from ash deposition would include reduced soil water content, reduced pH due to the acidity of the volcanic ash and reductions in soil organic matter (SOM), due to the high concentration of inert material (silicon dioxide) present in the ash. Taken together, we further predicted that the alterations in the abiotic conditions and direct negative effects on soil biota

would reduce ecosystem processes including microbial enzymatic activity and litter decomposition.

We were able to quantify the impact of the volcanic eruption by comparing pre- and post-eruption time points in the same study site, with nearly identical methodology in the 2 years. Additionally, we focused on the effect of ash on functional aspects of the microbial community under controlled conditions to provide possible mechanistic insights into the impact of this disturbance on carbon and nutrient turnover in this semi-arid ecosystem.

## Materials and methods

### STUDY SITE

This study was conducted in the Meliquina Valley (40°26'S 71°13'W), 40 km south from San Martín de los Andes, in the Neuquén province of Argentina. The site is located at an elevation of 906 m and corresponds to a semi-arid ecosystem with an average annual rainfall of 1100 mm, 80% of which occurs during fall and winter [Autoridad Interjurisdiccional de las Cuencas (AIC) 2009; Araujo & Austin 2015]. Average annual temperature is 8.9 °C with minimum average of -0.9 °C in winter and maximum average of 22.6 °C in summer [Autoridad Interjurisdiccional de las Cuencas (AIC) 2009]. Soils are Mollisols derived from volcanic ash and modified by transport and mixing with river sand and silt (Etchevehere & Dimitri 1972) with a xeric moisture regime (Ferrer & Irrisarri 1990). Natural vegetation is a semi-arid woodland of *Nothofagus antarctica* (G. Forst.) Oerst with a shrub-grass understory dominated by *Mulinum spinosum* Pers. and perennial grasses of *Pappostipa* spp. (Trin. & Rupr.) (Fig. 1, Hess & Austin 2014; Araujo & Austin 2015). A large fraction of the original natural vegetation in the valley, approximately 4800 ha in total, has been replaced with exotic woody species in plantations (Gyenge, Fernández & Schlichter 2008; Licata *et al.* 2008), especially ponderosa pine (*Pinus ponderosa* Doug. ex. Laws). Rainfall data were obtained through the Autoridad Interjurisdiccional de las Cuencas (AIC) of the Limay, Neuquén and Negro watersheds for the



**Fig. 1.** Study site in Meliquina Valley, Argentina, after the eruption of the Puyehue volcano in December 2011. This site is approximately 70 km from the epicentre of the eruption. The area is a mixture of natural woodland vegetation and exotic ponderosa pine (*Pinus ponderosa*) plantations. Panel insert shows a soil profile with ash deposition in the natural woodland vegetation.



monitoring site of Lago Meliquina (40°23'2.1''S 71°15'45.6''W), which is 8 km from the study site.

In June 2011, this site was affected by the eruption of the Puyehue-Cordón Caulle, with fine grain ash deposited in all areas at depths from 3 to 10 cm. The mineral composition was dominated by volcanic glass (SiO<sub>2</sub>), with low aluminosilicate content (Bermúdez & Delpino 2011), and had a geochemical signature similar to the previous eruption of this volcano in 1960 (Daga *et al.* 2014). In addition, the ash had a pH that varied between 6.2 and 6.5, with low electrical conductivity and high water retention capacity (Cremona, Ferrari & López 2011). Bioavailable nutrient content was extremely low, with 0.04% carbon (C), 0.006% nitrogen (N) and 3.1–8.5 ppm of phosphorus (P) (Cremona, Ferrari & López 2011).

#### FIELD SAMPLING

We quantitatively assessed soil microbial and faunal communities in two vegetation types, a natural woodland and an adjacent area of 35-year-old *P. ponderosa* plantation (for details and site description, please see Hess & Austin 2014; Araujo & Austin 2015). Soil and litter samples were taken on a plot of 50 × 50 m in each vegetation type at the peak of the growing season in December 2009 and January 2010 (prior to the eruption), and in December 2011 and January 2012 (6 months after the eruption). In all cases, results obtained post-eruption were compared with data obtained in the summer of 2009–2010 before ash deposition, directly comparing the same type of vegetation (natural vegetation or pine plantation).

In both sampling periods (and in both vegetation types), a total of eight 50-m equidistant transects were located. Four of the transects were used for the collection of soil, litter and the placement of pitfall traps for ground-dwelling arthropods (explained in the following paragraph) and four were used for nematode analysis. For soil and litter, two soil and litter samples were collected for each transect ( $N = 8$ ) at random points. At each sampling point, the depth of the ash layer was measured using a ruler. Mineral soil was sampled using plastic cylinders of 6 cm diameter to 10 cm depth (ash layer and plant debris was removed prior to soil sampling). For litter sampling, senescent plant material on the soil surface was collected from within a 10 × 10 cm frame. Samples were transferred, in hermetically sealed bags and refrigerated, until processing at the laboratory [Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA-CONICET), Faculty of Agronomy, Buenos Aires].

Nematodes were sampled by taking cores ( $N = 10$ ) of soil using a 3.5-cm-diameter plastic cylinder (0–10 cm depth) following transects in a zigzag manner (Chaves & Torres 1993) along the four transects that were not used for soil and litter sampling. For the 2010 pre-eruption sampling, all 40 soil cores from each vegetation type were pooled in a single composite sample due to logistic constraints on identification of nematode populations and functional types. For the 2012 sampling, composite samples were made by pooling 50 g of soil from each transect into one composite sample, repeated three times ( $N = 3$  for each vegetation type). This change in the sampling protocol between 2010 and 2012 was due solely to logistic differences in the ability for processing samples, and an effort to increase the precision of the nematode analysis.

Ground-dwelling arthropods were sampled using pitfall trapping (Gist & Crossley 1973) used to estimate the abundance of active soil surface invertebrates. Each pitfall trap consisted of a 3.5 cm diameter × 13 cm deep plastic container, placed in a hole where the lip of the container was flush with the soil surface. We filled the container with a solution of water with 50% propylene glycol, a low volatility preservative. To prevent interference at the entry point of the traps due to plant debris, rain, or capture by predators, we covered the traps with small transparent plastic

roofs placed approximately 15 cm above the traps (Fig. S1, Supporting information). Twelve pitfall traps per plot were placed along four equidistant 50-m transects at random points along each transect, but always least 4 m away from each other. Installed traps were left undisturbed in the field for approximately 2 months in both years prior and after the volcanic eruption (54 and 70 days, respectively).

#### LABORATORY ANALYSES AND TAXONOMIC DETERMINATIONS

##### *Microbial biomass and enzymatic activity*

In the laboratory, we determined soil gravimetric water content, litter water content, pH, organic matter, soil microbial biomass and extracellular enzyme activity in soil and litter. The pH of the ash collected at the site was also measured. To determine the gravimetric water content, soil was sieved using a 2-mm sieve, and 10 g of soil were placed in an oven at 105 °C for 48 h. For litter water content, 1–200 g litter was weighed and dried in the oven at 60 °C for 48 h. For soil pH, we used 5 g of soil with 10 mL of distilled water (1 : 2 ratio), and for litter pH, we homogenized 1.2 g of litter with 75 mL of distilled water with a Multiquick hand blender (Braun GmbH, Berlin, Germany). Soil and litter pH were measured with an electronic pH meter (Ultra Basic 300728.1; Denver Instrument Company, New York, NY, USA). Soil (400 mg) and litter (200 mg) samples were ground and combusted in a muffle furnace at 450 °C for 4 h for determination of organic matter content (Harmon, Nadelhoffer & Blair 1999).

Microbial biomass was assessed using a chloroform fumigation–extraction method (Vance & Brookes 1987) adapted to the study site (Gonzalez-Polo & Austin 2009). Fifty grams of soil was fumigated with chloroform for 24 h; labile carbon was extracted by shaking the samples with 0.5 M K<sub>2</sub>SO<sub>4</sub> solution for 1 h and then filtering them. Total microbial biomass carbon was analysed by digestion with K<sub>2</sub>S<sub>2</sub>O<sub>8</sub> and then titrated double endpoint method using 0.025 M HCl with an automated titrator (Mettler Toledo DL 15, Schwerzenbach, Switzerland). Microbial biomass values were calculated as the difference between fumigated and unfumigated extractable C concentrations corrected for extraction efficiency, using a standard  $k$  constant of 0.45 (Jenkinson, Brookes & Powlson 2004).

We evaluated potential activity of four extracellular enzymes:  $\beta$ -glucosidase (Sinsabaugh *et al.* 1999), phenol oxidase (POX) (Hendel, Sinsabaugh & Marxsen 2005), involved in the degradation of labile and recalcitrant carbon, respectively, glycine aminopeptidase (GAP) and phosphatase (Sinsabaugh *et al.* 1999), which are associated with the mineralization of nitrogen and phosphorus, respectively. The substrate 4-nitrophenyl- $\beta$ -D glucopyranoside was used for  $\beta$ -glucosidase, 3,4-dihydroxy-L-phenylalanine for POX, glycine *p*-nitroanilide for GAP and 4-nitrophenyl phosphate for phosphatase. Substrates were dissolved in Tris buffer (pH 7.2) for soil and acetate buffer (pH 5.5) for litter to simulate more closely the pH conditions of soil and litter from the study site. Samples were agitated and incubated for 2 h at ambient temperature (*c.* 24 °C). Absorbance was read at 460 nm for POX and at 410 nm for other enzymes with SP1105 spectrophotometer (Spectronic Instruments, VWR, Boston, MA, USA). All results are reported in  $\mu$ mol of product obtained per gram dry soil or dry litter, as appropriate.

##### *Identification of soil fauna*

For nematodes, each composite sample was sieved and homogenized and nematodes were extracted from 100 cm<sup>3</sup> of soil by the centrifugation technique (Caveness & Jensen 1955). Nematodes

were counted, identified and assigned to trophic groups (bacterial and fungal feeders, omnivores, root feeders and predators), based on their known feeding habits and oesophageal morphology according to Steinberger & Sarig (1993) and Yeates *et al.* (1993). Identifications were made using an Olympus SZ51 zoom stereo microscope and an Olympus CX31 biological microscope (Olympus Corporation, Tokyo, Japan).

For ground-dwelling arthropods, all adult individuals present in the pitfall traps were counted and identified to the taxonomic resolution of order using a Nikon SMZ800 zoom stereomicroscope (Nikon Instruments, Tokyo, Japan) with appropriate taxonomic keys for identification of arthropods of Argentina (Crespo *et al.* 1999). Abundance was corrected to a per day basis to account for the slight difference in sampling time of the pitfall traps in the 2 years. For community analysis, orders of arthropods which represented <1% of the total number of individuals found were grouped in the category of 'others' which included individuals from the orders Heteroptera, Mecoptera, Orthoptera, Psocoptera, Scorpionida, Solifuga, Thysanoptera as well as all other unidentified individuals.

#### SIMULATED ASH DEPOSITION UNDER CONTROLLED CONDITIONS

We installed a manipulative experiment in the experimental field site of IFEVA-CONICET, School of Agronomy, Buenos Aires (34°36'S 58°22'W). The climate is temperate humid with average temperature of 16.9 °C (Vivanco & Austin 2006). The experiment consisted of 10 perforated plastic boxes (55 cm length × 36 cm width × 18 cm height), in which we placed 2 kg of soil collected in the vicinity of the study site, free of volcanic ash, mixed with 2 kg of sand. In the boxes, after installing the soil mixture, we installed 15 × 15 cm litterbags of 2-mm fibreglass mesh with leaf litter of three species (1.500 g): *N. antarctica*, the native tree in the woodland ecosystem, *P. ponderosa* and *Populus nigra* L., which was a litter substrate not present in the two ecosystems in Patagonia, and which we have used in other experiments as a common litter substrate (Vivanco & Austin 2008, 2011; Araujo & Austin 2015). All litter came from the site (or in the case of *P. nigra*, an adjacent ranch very near the study site). Prior to installation in litterbags, litter was carefully cleaned and selected to include only recently senesced, intact litter. Two duplicate litterbags of each species were installed in each box, one for measuring enzyme activity ( $N = 5$ ) and the other to calculate mass loss ( $N = 5$ ). In one half of the boxes ( $N = 5$ ), we applied a treatment that consisted of 2 kg of volcanic ash (collected from our specific study site in the months just following the eruption) that was distributed uniformly to a 5-cm depth that was similar to that found in the field site. The remaining boxes were the control treatment without simulated ash deposition. Boxes were lined with 80% shade cloth to avoid the effects of photodegradation on litter decomposing on the exposed soil surface (Austin, Araujo & Leva 2009). Boxes were placed in pairs under constructed plastic film screens (1.3 × 1.2 m) using aluminium rods and bolts to maintain the plastic film stretched tight and placed the screens approximately 40 cm above the soil boxes to prevent wetting from natural rain events (Austin, Araujo & Leva 2009). Boxes were irrigated weekly with water equivalent to a precipitation event of 10 mm (approximately 1.5 L), and twice weekly during high temperature weeks. We measured surface temperature (ash or soil) with a Fluke 63 infrared thermometer (Fluke Corporation, Everett, WA, USA) on four dates; all measurements were performed at midday with three replicate measurements in each box.

The experiment was initiated in August of 2012, and we collected litterbags in mid-December for a total of 143 days of incubation. Soil samples were taken at the same time as the litterbag collection using plastic cylinders of 5 cm diameter, previously removing the

ash layer in the ash deposition treatments. Samples were stored in ziploc bags at 4 °C. We determined gravimetric water content, pH, organic matter, microbial biomass and enzyme activity of the four enzymes as described above in the field experiment, using in all cases the same methods with the exception of soil pH, where we used a ratio of 1 : 5 for soil to distilled water. Litter was removed from the litterbags and cleaned to remove foreign debris (soil, ash, plant material of other species, etc.). Litter used for enzyme assays was placed in ziploc bags and kept in the refrigerator until analysis, which was performed within 48 h of harvest. Litter used for mass loss measuring was weighed, dried in a 60 °C oven for 48 h and reweighed to determine water content and mass loss. Then, the material was ground, and subsamples were combusted in a muffle furnace at 450 °C to determine inorganic matter content and correcting for ash contamination (Robertson *et al.*, 1999). We calculated organic matter loss for each litterbag.

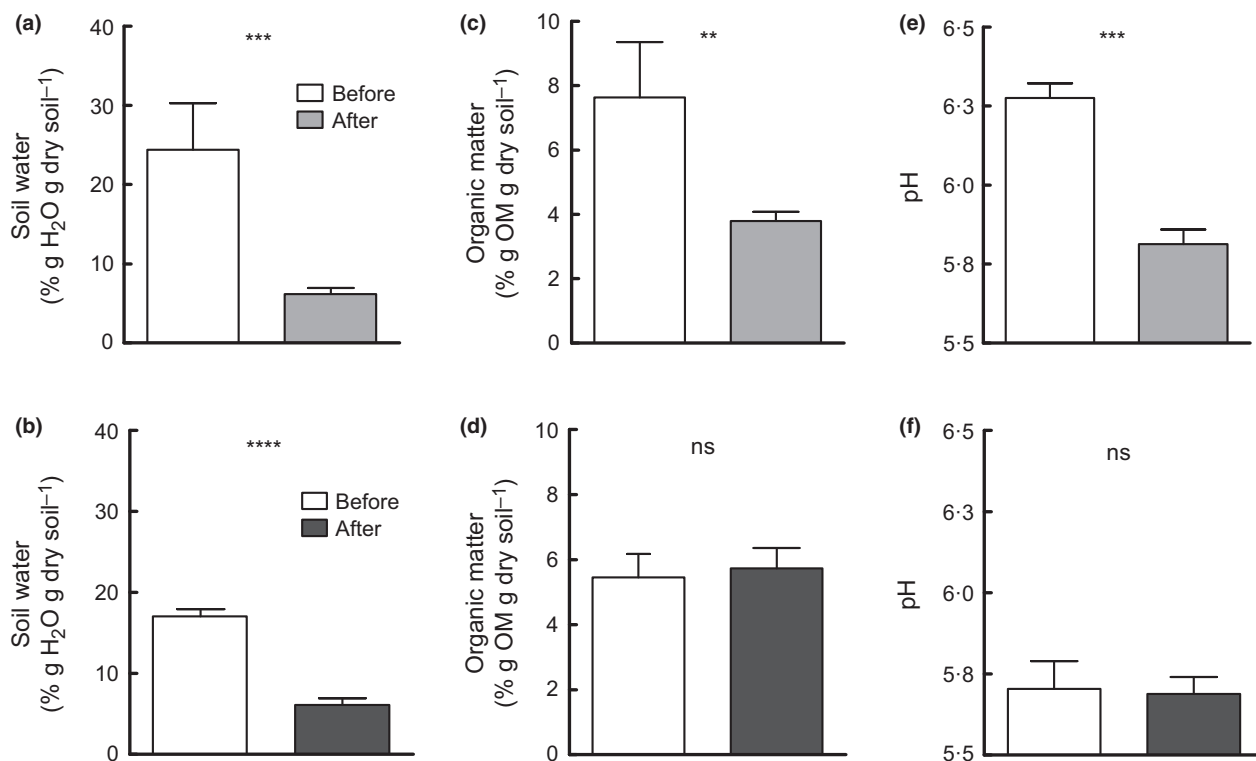
#### STATISTICAL ANALYSIS

Data from the field (soil environmental characteristics, microbial biomass, soil faunal abundance) were assessed by one-way ANOVA using date as factor (before and after ash deposition). Differences between vegetation types were not possible to evaluate because there was a single plot for each vegetation type, and true replication was not feasible. Analysis of data from the manipulative experiments was performed by one-way ANOVA, for soil data, and two-way ANOVA, for litter data, with ashes and litter type (species) as factors. *Post hoc* comparisons were performed with a Tukey test. Data were log-transformed in cases where the assumptions of normality and homogeneity of variances were not met with untransformed data. Simple linear regressions were fitted with field data in order to relate the extracellular enzyme activity with soil or litter water content. To determine the degree of association between the variables measured in the manipulative experiment, we used Pearson correlation indices. In all cases, the level used for determination of significant differences was  $\alpha \leq 0.05$ . Data analyses were performed using Infostat version 2009 (National University of Córdoba, Statistics and Design, Córdoba, Argentina) and STATISTICA 8.0 (StatSoft, Inc., Tulsa, OK, USA).

## Results

#### EFFECTS OF ASH DEPOSITION ON ENVIRONMENTAL CHARACTERISTICS

Annual precipitation in the 2 years of measurement was variable; the year prior to ash deposition was considerably wetter than the year of volcano eruption, with measured annual rainfall of 1446 and 946 mm before and after ash deposition, respectively [Autoridad Interjurisdiccional de las Cuencas (AIC) 2009, 2010, 2011]. The depth of the ash layer in the study site was  $4.76 \pm 0.65$  ( $\pm$ SE) cm in the natural woodland vegetation and  $2.04 \pm 0.26$  cm in the pine plantation. Soil water content was substantially higher before ash deposition in both vegetation types ( $32 \pm 5\%$  before and  $11 \pm 1\%$  after in natural vegetation,  $P = 0.0004$ ;  $40 \pm 5\%$  before and  $12 \pm 1\%$  after in pine plantation,  $P < 0.0001$ , Fig. 2a,b). Litter water content was also higher before ash deposition in both vegetation types ( $46 \pm 11\%$  before and  $12 \pm 1\%$  after in natural vegetation,  $P = 0.0005$ ;  $53 \pm 8\%$  before and  $14 \pm 1\%$  after in pine plantation,  $P < 0.0001$ , Table 1). In the



**Fig. 2.** Environmental characteristics of soil before (white bars) and after (shaded bars) ash deposition in natural vegetation (a, c, e) and pine plantation (b, d, f). Water content (%) (a, b), organic matter at 0–10 cm (%) (c, d) and pH (e, f). Bars indicate mean + SE. Asterisks indicate level of significance: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , \*\*\*\* $P < 0.0001$ , ns: not significant.

**Table 1.** Litter water content (WC, % dry mass), organic matter (OM, %) and pH in natural vegetation (semi-arid woodland) and an adjacent pine plantation before and after ash deposition as a result of the Puyehue eruption in June 2011. Means  $\pm$  SE (standard errors) are shown

Vegetation type	WC (%)	OM (%)	pH
Natural vegetation			
Before	32 $\pm$ 5	56 $\pm$ 8	5.3 $\pm$ 0.18
After	11 $\pm$ 1	79 $\pm$ 3	5.2 $\pm$ 0.17
<i>P</i> value	0.0004	0.0145	0.5134
Pine plantation			
Before	40 $\pm$ 5	72 $\pm$ 8	5.5 $\pm$ 0.06
After	12 $\pm$ 1	88 $\pm$ 2	5.3 $\pm$ 0.19
<i>P</i> value	<0.0001	0.044	0.3574

manipulative experiment, simulated ash deposition confirmed the pattern observed in the field, with significant decreases in soil water content ( $P < 0.001$ , Table 2), while contrasting results were seen in litter with significantly increased water content ( $P = 0.0047$ , Table 3). In the field, the effect of ash on organic matter and pH in soil was dependent on the vegetation type, with lower organic matter ( $P = 0.008$ ) and pH ( $P = 0.0002$ ) after ash deposition only in natural vegetation (Fig. 2c,e), while in the pine plantation, organic matter and pH in soil did not differ (Fig. 2d,f). No significant differences between treatments in SOM, pH or soil surface temperature were observed in the soils of the manipulative experiment (Table 2).

**Table 2.** Soil environmental and biological variables with simulated ash deposition. Microbial biomass is expressed in  $\mu\text{g C g dry soil}^{-1}$  and potential enzyme activities in  $\mu\text{mol product g dry soil}^{-1} \text{ h}^{-1}$

	– ash	+ ash	<i>P</i> value
Environmental variables			
WC (%)	16.0 $\pm$ 0.8	11.2 $\pm$ 0.2	<0.001
OM (%)	2.6 $\pm$ 0.1	2.5 $\pm$ 0.1	ns
pH	6.30 $\pm$ 0.02	6.31 $\pm$ 0.03	ns
Temperature ( $^{\circ}\text{C}$ )	39.8 $\pm$ 0.9	41.1 $\pm$ 0.9	ns
Biological variables			
MB	46.6 $\pm$ 10.6	46.1 $\pm$ 14.5	ns
BG	0.302 $\pm$ 0.051	0.204 $\pm$ 0.047	ns
POX	0.062 $\pm$ 0.006	0.073 $\pm$ 0.009	ns
GAP	0.145 $\pm$ 0.043	0.085 $\pm$ 0.030	ns
AP	1.050 $\pm$ 0.166	0.738 $\pm$ 0.116	ns

WC, water content; OM, organic matter; BG,  $\beta$ -glucosidase; POX, phenol oxidase; GAP, glycine aminopeptidase; AP, acid phosphatase.

Mean  $\pm$  SE for each treatment is shown.

#### EFFECTS OF ASH DEPOSITION ON SOIL BIOTA

Total abundance of ground-dwelling arthropods increased significantly after the volcanic eruption in both vegetation types (natural vegetation,  $P < 0.0001$  and pine plantation,  $P = 0.0002$ ): in natural vegetation, the increase was more than twofold (74  $\pm$  12.8 and 253  $\pm$  31.6

**Table 3.** Litter water content (% dry mass), organic matter (%) and potential enzyme activities in litter ( $\mu\text{mol product g dry mass}^{-1} \text{ h}^{-1}$ ) with simulated ash deposition

	WC	OM	BG	POX
<i>Nothofagus antarctica</i>				
– ash	7.8 $\pm$ 0.4	92 $\pm$ 0.7 <sup>a</sup>	31.9 $\pm$ 5.3	0.26 $\pm$ 0.26
+ ash	9.1 $\pm$ 0.4	67 $\pm$ 1.0 <sup>c</sup>	14.1 $\pm$ 1.8	1.87 $\pm$ 0.82
<i>Pinus ponderosa</i>				
– ash	6.5 $\pm$ 0.6	95 $\pm$ 0.3 <sup>a</sup>	20.5 $\pm$ 4.1	0.30 $\pm$ 0.18
+ ash	7.9 $\pm$ 0.4	92 $\pm$ 0.5 <sup>a</sup>	11.3 $\pm$ 0.6	1.75 $\pm$ 0.35
<i>Populus nigra</i>				
– ash	7.5 $\pm$ 0.6	80 $\pm$ 0.8 <sup>b</sup>	44.4 $\pm$ 5.1	0.34 $\pm$ 0.09
+ ash	8.6 $\pm$ 0.5	63 $\pm$ 2.3 <sup>c</sup>	26.7 $\pm$ 6.1	0.76 $\pm$ 0.17
Ash	<0.01	<0.0001	<0.0001	<0.001
Litter	<0.05	<0.0001	<0.001	ns
A $\times$ L	ns	<0.0001	ns	ns

Abbreviations are shown in Table 2.

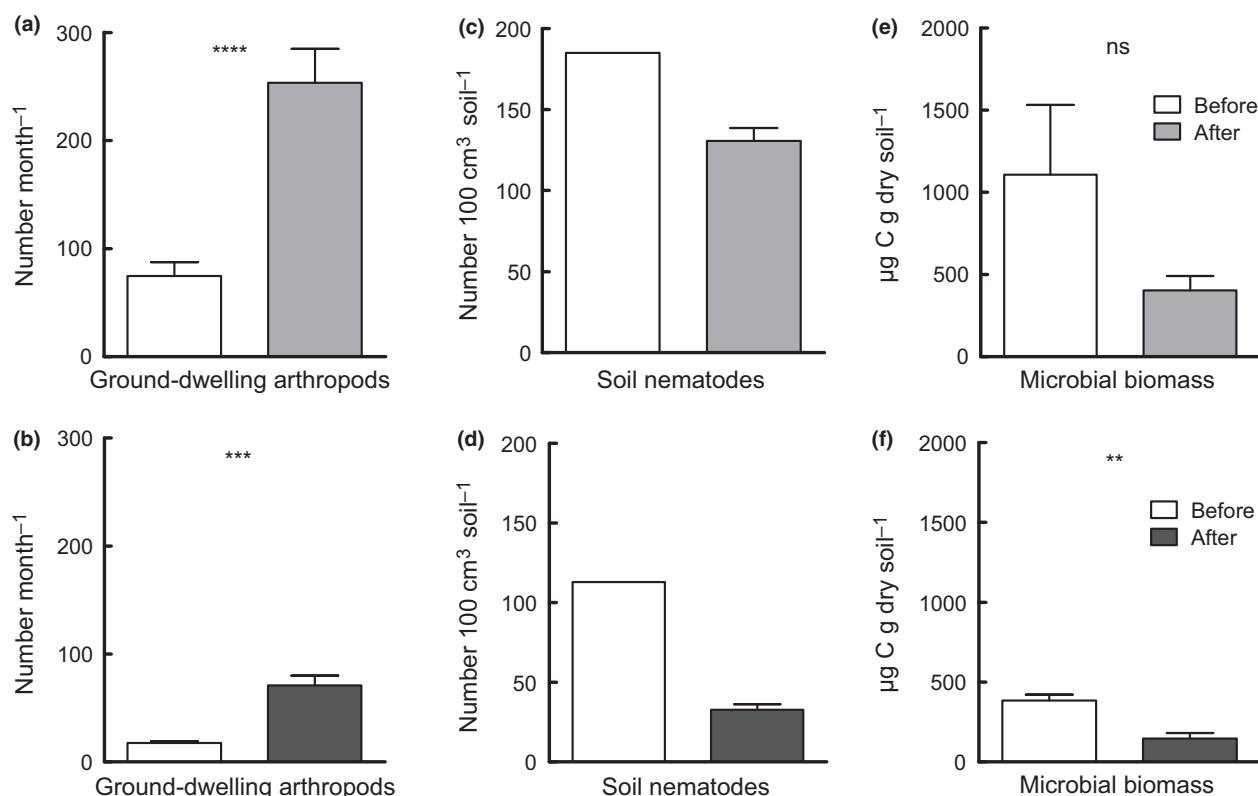
Mean  $\pm$  SE for each treatment is shown.

individuals trap<sup>-1</sup> month<sup>-1</sup> before and after ash deposition, respectively, Fig. 3a). This overall response involves several orders that significantly increased their absolute abundance after the ash deposition including Hymenoptera (ants), Acari (mites), Homoptera (aphids, leafhoppers, mostly phytophagous insects) and Araneae (spiders), while an important group of detritivores, Archaeognatha, was not detected after the eruption (Fig. 4a, Table S1). In the

pine plantation, the increase was threefold, although overall abundance of ground-dwelling arthropods was lower in the pine plantation relative to the native vegetation ( $17 \pm 1.5$  and  $71 \pm 9.2$  individuals trap<sup>-1</sup> month<sup>-1</sup> before and after ash deposition, respectively, Fig. 3b). Similar to the natural woodland, Acari, Homoptera and Araneae significantly increased their absolute abundance ( $P < 0.01$  in all cases, Table S1) and Archaeognatha was not observed after ash deposition (Fig. 4b, Table S1,  $P < 0.01$ ).

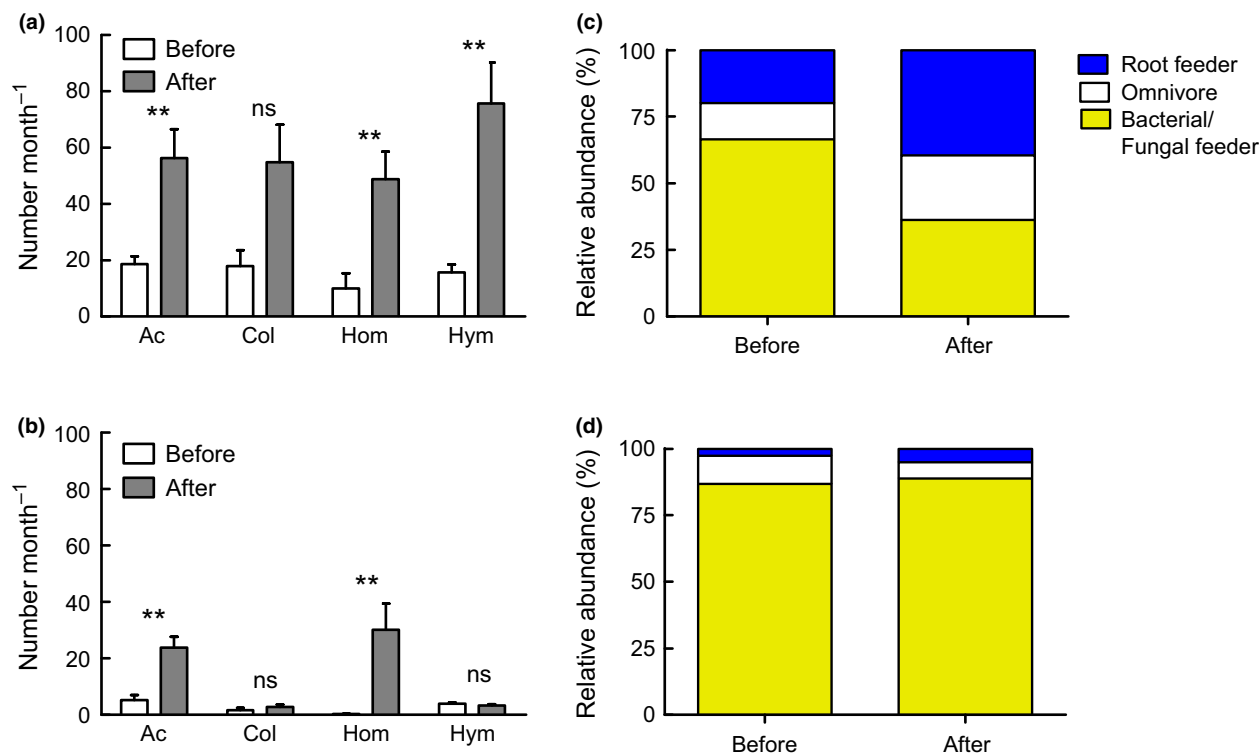
Relative abundance (% of total) of orders of ground-dwelling arthropods changed after ash deposition differentially in natural vegetation than in the pine plantation. In the natural vegetation (Fig. S1), overall relative abundances were similar, although Hymenoptera and Homoptera increased in relative proportion to the other arthropods after the eruption. Most noteworthy was the Archaeognatha (detritivores), which were an important part of the community prior to the eruption (9.3%), but completely disappeared after ash deposition. In the pine plantation, changes in community composition were more evident (Fig. S1), with a decline in the relative proportion of Hymenoptera and Coleoptera after ash deposition, while Homoptera increased dramatically from 1.5% before to 42% of the soil faunal community.

In contrast to the response of ground-dwelling arthropods populations, nematode abundance decreased after ash



**Fig. 3.** Abundance of soil biota before (white bars) and after (shaded bars) the eruption of the Puyehue volcano in natural woodland vegetation (a, c, e) and pine plantation (b, d, f). Ground-dwelling arthropods are expressed as the number of individuals per pitfall trap month<sup>-1</sup> (a, b), soil nematodes [number of individuals 100 cm<sup>3</sup> soil<sup>-1</sup> (SE is shown only for the post-eruption date, see Field Sampling for details on sampling protocol)] (c, d) and soil microbial biomass ( $\mu\text{g C g dry soil}^{-1}$ ) (e, f). Bars indicate mean + SE. Asterisks indicate level of significance: \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , \*\*\*\* $P < 0.0001$ , ns: not significant.





**Fig. 4.** Abundance of soil fauna groups before and after ash deposition in natural vegetation and in pine plantation sites. Left hand panels are (a) absolute abundance of the most abundant orders of ground-dwelling arthropods orders expressed as number of individuals per trap per month: Acari (Ac), Collembola (Col), Homoptera (Hom) and Hymenoptera (Hym) in a) natural vegetation and (b) pine plantation. Each bar represents mean + SE and asterisks indicate level of significance: \*\* $P < 0.01$ , ns: not significant. Right hand panels are relative abundance of nematode functional groups expressed as % of total in (c) natural vegetation and (d) pine plantation.

deposition by 29% in natural vegetation ( $185$  and  $131 \pm 8.1$  individuals  $100 \text{ cm}^{-3}$  soil before and after ash deposition, respectively; see Field Sampling for details on differences in sample size between events) and more markedly in pine plantation, where nematodes decreased by 71% ( $113$  and  $32.8 \pm 3.5$  individuals  $100 \text{ cm}^{-3}$  soil, respectively; see Field Sampling for details). No predatory nematodes were found in either type of vegetation. Relative abundances (% of total) of trophic groups found in natural vegetation (Fig. 4c) demonstrated strong community responses to the ash deposition; bacterial and fungal feeders declined from 66 to 36% of the total nematode community after ash deposition. In contrast, there was a substantial increase in proportion and number of root feeders, from 20% before to nearly 40% of the community after ash deposition (Table S2, Fig. S2). In spite of large changes in the overall abundance, there was little response on the relative abundance of functional groups in the pine plantation (Fig. 4d) with only a modest increase in the relative proportion of phytophagous nematodes after ash deposition.

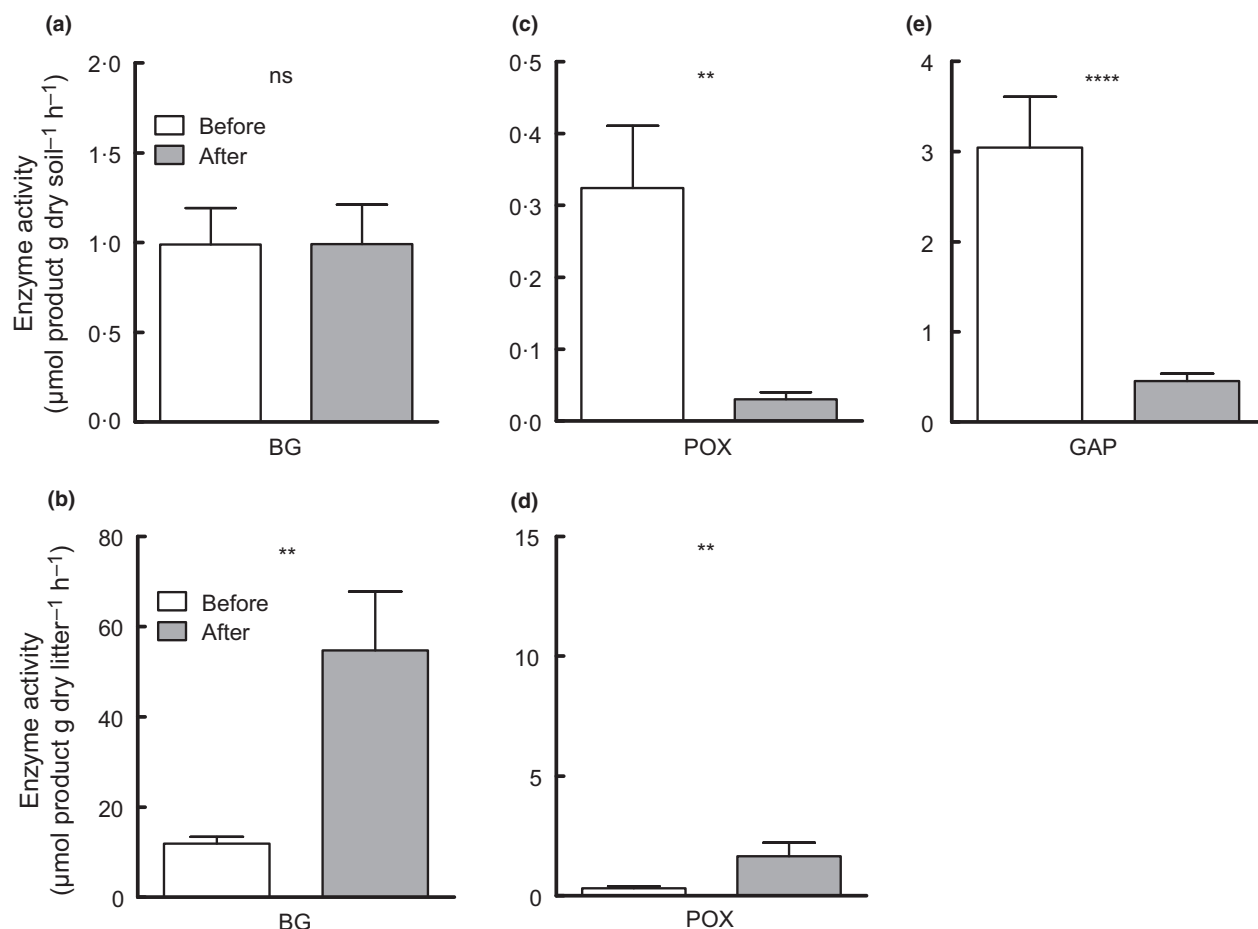
Finally, soil microbial biomass differed significantly between evaluated dates in the pine plantation, which decreased markedly after ash deposition ( $P = 0.001$ ), while similar trends observed in the natural vegetation were not statistically significant (Fig. 3e,f). There was no detectable difference in the soil microbial biomass in the manipulative experiment (Table 2).

#### EFFECTS OF ASH DEPOSITION ON ECOSYSTEM PROCESSES

In both the natural woodland and the pine plantation, no significant differences were observed in soil  $\beta$ -glucosidase (BG) activity (Figs 5 and 6), but we did find differences in activity of two soil enzymes, POX and GAP, which decreased significantly after ash deposition (Figs 5 and 6). In the manipulative experiment, no differences between treatments were found for extracellular enzyme activity in soil (Table 2). Evaluation of the relationship between soil water content and enzymatic activity yielded significant relationships for all enzymes before ash deposition (BG:  $y = 0.0288x + 0.2832$ ,  $r^2 = 0.41$ ,  $P = 0.01$ ; POX:  $y = 0.0119x + 0.029$ ,  $r^2 = 0.64$ ,  $P = 0.0005$ ; GAP:  $y = 0.0752x + 0.5017$ ,  $r^2 = 0.57$ ,  $P = 0.003$ ). In the year after ash deposition, no significant relationship between these variables was found.

In contrast to the decline in soil enzymatic activity, litter enzymatic activities were consistently and significantly higher after ash deposition in natural vegetation (Fig. 5b, d) and in the pine plantation (Fig. 6b,d), although no relationship between litter enzyme activities and litter water content was observed. In the manipulative experiment, we found significant effects of simulated ash deposition on the activity of three of the four enzymes measured in litter; BG activity decreased ( $P < 0.0001$ ), while POX increased





**Fig. 5.** Enzyme activities in soil (a, c, e) and litter (b, d) before (white bars) and after (shaded bars) ash deposition in natural woodland vegetation.  $\beta$ -glucosidase activity (BG) (a, b), phenol oxidase activity (POX) (c, d) and glycine aminopeptidase activity (GAP) (e). Bars indicate mean + SE. Asterisks indicate level of significance: \*\* $P < 0.01$ , \*\*\*\* $P < 0.0001$ , ns: not significant. Note the difference in scale of x-axis between soil and litter.

( $P = 0.0004$ , Table 3). Effects of simulated ash deposition on acid phosphatase (AP) activity were significant ( $P = 0.0107$ ) but differed among the species with a significant interaction of  $A \times L$  ( $P = 0.002$ ) (Table S4).

Finally, litter organic matter loss was strongly stimulated by simulated ash deposition, with a nearly fourfold increase in decomposition (Fig. 7). Additionally, there was an ash by litter species interaction ( $A \times L$ ,  $P = 0.0002$ ), which indicated that the magnitude of the stimulation of decomposition differed among species, with the largest change seen in *N. antarctica* and *P. ponderosa* litter, while *P. nigra* decomposition responded less strongly to the simulated ash deposition.

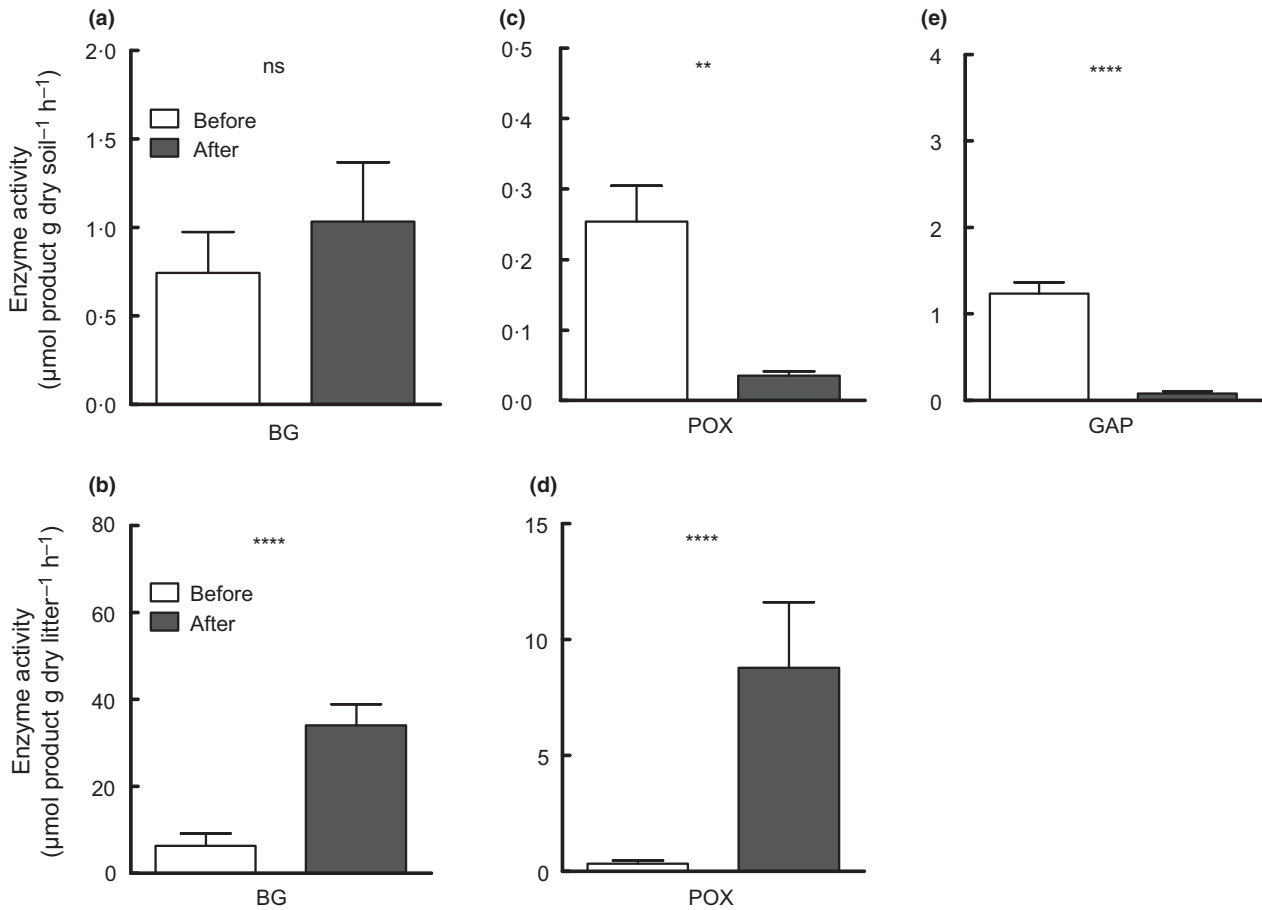
## Discussion

### ASH DEPOSITION AND WHAT RESIDES IN THE SOIL

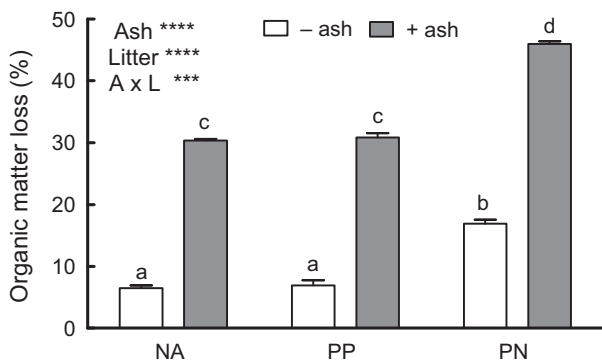
The majority of studies have reported negative impacts of ash deposition on different groups of organisms in terrestrial and aquatic ecosystems (Edwards & Schwartz 1981; Ghermandi & González 2012; Wolinski *et al.* 2013), with

notable reductions in population size (Elizalde 2014) and reproduction in the years following large-scale eruptions. In particular, there is evidence that ash deposition can significantly increase mortality of insects even at great distances from a volcanic eruption. Recently published descriptions of the aftermath of the eruption of the Puyehue volcano appear to demonstrate negative impacts on invasive wasps (Masciocchi *et al.* 2013), non-native bees (*Apis mellifera*) (Martínez *et al.* 2013) and plant–pollinator and plant–herbivore interactions (Chaneton *et al.* 2014; Morales *et al.* 2014).

While almost nothing is known regarding the response of soil nematode populations to volcanic eruptions, our results add to the general pattern of negative impacts on some soil organisms due to the ash deposition. This contrasts with one of the only direct evaluations of volcanic ash of root-knot nematodes, which showed that populations were unaffected by volcanic ash from Mt. St. Helens in a laboratory experiment (O'Bannon & Santo 1981). Although nematodes have a wide array of strategies to avoid or survive stressful environmental conditions including dormancy, alteration of sex ratios and



**Fig. 6.** Enzyme activities in soil (a, c, e) and litter (b, d) before (white bars) and after (shaded bars) ash deposition in pine plantation. Abbreviations are shown in Fig. 5. Bars indicate mean + SE. Asterisks indicate level of significance: \*\* $P < 0.01$ , \*\*\*\* $P < 0.0001$ , ns: not significant. Note the difference in scale of x-axis between soil and litter.



**Fig. 7.** Organic matter loss of *Nothofagus antarctica* (NA), *Pinus ponderosa* (PP) and *Populus nigra* (PN) litter without and with simulated ash deposition. Bars indicate mean + SE. Asterisks indicate level of significance: \*\*\* $P < 0.001$ , \*\*\*\* $P < 0.0001$ . Different letters indicate significant differences for *post hoc* Tukey test ( $P \leq 0.05$ ).

even anhydrobiosis (Treonis, Wall & Virginia 2000; McSorley 2003), these organisms are also known for their rapid response to changing resource availability and hence are often used as bioindicators for soil conditions

(Yeates *et al.* 1993; Bongers & Bongers 1998). The significant reduction in nematode abundance after ash deposition in both types of vegetation may reflect resource scarcity, in particular due to the fact that the reduction was predominantly driven by the reduction in bacterial and fungal feeders, which coincided with reductions in microbial biomass after ash deposition (Fig. 3e,f). On the other hand, the community composition changed to reflect a higher proportion of phytophagous (root-feeding) nematodes, particularly in the natural vegetation where nearly 40% more individuals were found (Fig. 4c, d, Table S2). This increase may also be driven by the reduction in soil microbes that can regulate root-feeding nematode populations (Rodríguez-Kabana, Morgan-Jones & Chet 1987; Akhtar & Malik 2000), or weakened plant defence in the light of the ash deposition, resulting in an increased importance of this particular functional group (Van Der Putten 2003).

Our original hypothesis was that in the aftermath of this volcanic eruption, the abundance and community composition of soil fauna would diminish due to previously observed patterns and to the demonstrated insecticide effect of ash on arthropod communities.

Nevertheless, the surprisingly large increases in ground-dwelling arthropods do mirror aquatic studies evaluating phytoplankton populations in lakes affected by this disturbance. Modenutti *et al.* (2013) found a significant increase in phytoplankton over pre-eruption years, which was attributed to improved resource availability of limiting phosphorus and the attenuation of harmful levels of solar UV radiation in the water column. In addition, the colonization of lupine species on Mt. St. Helens provided for an explosion of herbivorous insects in the years following the eruption, to the point where these insects impeded the colonization of the post-volcanic landscapes by prairie lupines (Fagan, Bishop & Schade 2004; Fagan *et al.* 2005).

The increase in the abundance of ground-dwelling arthropods could be due to a combination of factors, which are not mutually exclusive. One is the timing of the eruption, which occurred in late fall in a season in which many arthropods have reduced levels of activity. These organisms may have established refuges or were in a dormant state that provided protection from the ash deposition and therefore its potential insecticidal effects. Supporting this mechanism are recently published results suggesting some neutral effects on arthropod populations after the Puyehue eruption: abundance and species richness of ants (Hymenoptera) and beetles (Coleoptera) were relatively unaffected in grass–shrub steppe vegetation (Pirk 2014), and the elevation–abundance relationships of mountain beetles did not appear to be altered by the eruption and subsequent ash deposition (Ruggiero & Werenkraut 2014). The authors attributed this modest impact on the timing of the eruption, and low arthropod activity associated with cold temperatures. This factor was also considered to explain the survival of many arthropods after the Mount St. Helens eruption (Edwards & Sugg 2005). An additional factor to consider is that the ash layer may also reduce the temperature variation at the soil surface (Erickson & Edmonds 1994), resulting in a more favourable environment for survival and reproduction. These effects of seasonality may be important to incorporate in our conceptual models of large-scale disturbances.

A further possibility could be the negative effects on other arthropod groups, resulting in a decrease in predation pressure or alterations of plant–insect interactions. This possibility is consistent with the observed marked decline in the populations of predatory wasps after the Puyehue eruption (Masciocchi *et al.* 2013) and a reduction in insect herbivory (Chaneton *et al.* 2014). It seems clear that arthropods have multiple responses to the disturbances caused by volcanic eruptions (Bishop *et al.* 2005; Edwards & Sugg 2005; Chaneton *et al.* 2014; Ruggiero & Werenkraut 2014), and the generality that ash deposition functions as an insecticide negatively impacting all groups of arthropods may need to be broadened in the context of these results, particularly pertaining to ground-dwelling arthropods.

#### ASH DEPOSITION AND SOIL PROCESSES: EFFECTS ON WATER AND CARBON BALANCE

One of the most notable differences observed after ash deposition in the field was a significant reduction in soil moisture in both the natural woodland vegetation and the pine plantation. These effects are consistent with our hypothesis that predicted that the hydrophobic characteristics of the ash would inhibit water infiltration, in addition to acidifying the soil and reducing SOM. Similar results were found in studies conducted after the eruption of Mt. St. Helens, where soil moisture was reduced under areas of ash deposition (Erickson & Edmonds 1994; Antos & Zobel 2005). Despite the climatic variability inherent to field studies, direct support for the effects of ash deposition on soil water content comes from the manipulative experiment, which demonstrated clear and indisputable effects decreasing water content of the soil (Table 2). But simultaneously with the reduction in soil moisture in the soil layer was an increase in moisture in the litter layer, which generated a significant negative correlation between litter and soil water content (Tables 3 and S3). These differences suggest that volcanic ash functions as a barrier to impede water infiltration to the soil, but at the same time increases water retention in the litter layer that is in direct contact with the ash. The net effect is a differential effect of soil moisture on litter and soil compartments, which has not been considered previously with respect to the impact of ash deposition on microbial soil and litter activity.

The observed reduction in soil enzymatic activity is also consistent with results from Mt. St. Helens, which showed persistent long-term decreases on soil phosphatase and dehydrogenase enzymes, with ash deposition (Halvorson & Smith 2009). However, a direct causal connection between ash deposition, reduction in soil moisture and consequent declines in soil enzymatic activity must be interpreted with caution, given that the months prior to the first sampling before ash deposition were wetter than the sampling period after the volcanic eruption. Nevertheless, the demonstrated correlation between soil moisture content and enzymatic activity in the field prior to the eruption suggests that soil moisture variability, independently of ash impacts, may be a central control on soil enzymatic activity in these ecosystems. Additionally, in the natural vegetation, the reduction in SOM and changes in pH generated by ash deposition could have impacted soil enzymatic activity. It is clear that soil pH exerts direct effects on the activity of extracellular enzymes (Sinsabaugh *et al.* 2008), and concentrations of SOM are a limiting resource for soil microbial activity in these semi-arid ecosystems (Gonzalez-Polo & Austin 2009; Austin 2011). These factors could have contributed to the reduction in potential soil enzymatic activity independently of changes in water availability.

The strong stimulation of microbial enzymatic activity in litter and a fourfold increase in litter decomposition is a counterintuitive result from this study and contrasts sharply with the patterns observed in the soil. Similar,

but much smaller, responses to litter decomposition were found in Mt. St. Helens for several conifer species (Edmonds & Erickson 1994; Erickson & Edmonds 1994). Furthermore, the notable increase in litter decomposition observed in our experiment cannot be explained only by the fact that litterbags in the ash addition treatment were buried under the ash layer. If we compare our results with those from two field experiments conducted in Meliquina Valley where litterbags were incubated on the soil surface, similar to conditions prior to the eruption, and buried below-ground, comparable with ash addition treatment, this comparison shows that the increase in litter decomposition due to ash deposition simulation was considerably larger than the increase due to burial at 5 cm depth in the soil (Table 4). These results support the idea that micro-organisms respond to a range of environmental factors beyond water constraints including variation in substrate nutrient availability (Gonzalez-Polo & Austin 2009). Scarce availability of nutrients, such as that seen in the volcanic ash substrate, could stimulate the synthesis of enzymes to mobilize resources of complex substrates (Allison 2005; Sinsabaugh & Shah 2011). It is feasible that the deposition of ash, composed mainly of inert material, generated external cues for a novel low-nutrient environment for microbial populations, particularly in the litter layer, which effectively stimulated the production of extracellular enzymes for both complex carbon substrates and nutrient degradation. While not universally consistent across all enzymes, we did observe significant increases in BG and POX activity under field conditions (Figs 5b,d and 6b,d), and POX and AP activity in the simulated ash experiment for some litter treatments (Tables 3 and S4). This reinforces the idea that there may be external cues which overrides standard stoichiometric relationships present in the litter, and is consistent with the fact that, surprisingly, there was almost no difference in the decomposition of widely divergent litter qualities of pine, southern beech and aspen litters (Fig. 7, Gholz *et al.* 2000; Araujo & Austin 2015). These results demonstrating the complexity of the microbial response to this disturbance highlight the need for a stronger conceptual framework and improved understanding of the factors which stimulate or inhibit microbial enzymatic activity in the litter layer.

#### KEEP CALM AND CARRY ON: THE RESILIENCE OF SOIL BIOTIC COMMUNITIES

Volcanic eruptions are one of the major natural disturbances, and their effects on the structure and functioning of ecosystems are diverse and complex. Taken together, the bulk of the evidence presented in this study suggests that the principal effects of the eruption of Puyehue volcano resulted in the short-term stimulation of litter microbial activity and a marked increase in the populations of several groups of ground-dwelling arthropods. This surprising response contrasts directly with our hypotheses and suggests that the soil biota in these ecosystems appears to be both more ecologically resistant and resilient than previously thought. Qualitatively, it appears that the pine plantation, which is a highly modified ecosystem, did not differ in response to ash deposition when compared to the natural ecosystem, in spite of large direct impacts of the plantations on soil faunal community composition nitrogen cycling and litter decomposition (Hess & Austin, 2014; Araujo & Austin 2015). The effects of ash deposition do not appear to be multiplicative when combined with afforestation effects in this site, in contrast to what has been suggested for ecosystems subjected to both natural and anthropogenic disturbances (Paine, Tegner & Johnson 1998).

The stimulation of ash deposition on soil faunal populations and activity raises several points of interest. First, it seems that many large-scale disturbances are far from catastrophic for the affected ecosystem and appear to form a part of the temporal landscape of the ecosystem (Dale, Crisafulli & Swanson 2005). This seems particularly true in the case of ecosystems in the vicinity of the Puyehue volcano, which have experienced repeated volcanic eruptions and subsequent ash deposition in the last century (Daga *et al.* 2014). Based on the evidence from this study, it appears that the biotic component of these ecosystems has a substantial capacity to respond to these disturbances in short time frames, which is consistent with some of the other studies in the region in the aftermath of the eruption (Pirk 2014; Ruggiero & Werenkraut 2014). The previously unobserved increases in litter enzymatic activity and decomposition suggest that nutrient mineralization of litter and consequent nutrient availability will likely increase in

**Table 4.** Organic matter loss per day (%) of *Nothofagus antarctica*, *Pinus ponderosa* and *Populus nigra* litter in the ash deposition experiment (ash–, ash+) under controlled conditions and in two separate field experiments conducted at the same sites in Meliquina Valley. Fibreglass mesh litterbags were incubated on the soil surface (above; Araujo & Austin 2015) and buried below-ground (below; D. Gangi, A. González-Arzac, & A.T. Austin, unpublished data)

	Field Above-ground	Controlled –ash	Field Below-ground	Controlled +ash
<i>N. antarctica</i>	0.099 ± 0.023	0.046 ± 0.003	0.101 ± 0.010	0.212 ± 0.002
<i>P. ponderosa</i>	0.039 ± 0.015	0.048 ± 0.006	0.108 ± 0.007	0.216 ± 0.005
<i>P. nigra</i>	0.189 ± 0.017	0.118 ± 0.005	0.193 ± 0.013	0.321 ± 0.003

Mean ± SE for each treatment is shown.



the short term, and combined with the increased water holding capacity of the volcanic ash, it may have a positive impact on plant growth. As such, the biogeochemical resilience in the wake of this disturbance is somewhat surprising (McLauchlan *et al.* 2014), although equally rapid recovery has been predicted for lentic ecosystems of the region (Modenutti *et al.* 2013; Wolinski *et al.* 2013).

Secondly, the differential response of organisms may reflect the relative vulnerability to disturbance and in particular to ash deposition. It is noteworthy that the faunal groups that seem most negatively affected by the eruption were those that have direct contact with the component most affected by the ash, the soil. Soil nematodes, particularly bacterial and fungal feeders, were negatively impacted, which possibly reflects the interference caused by the ash to locate their food source. In addition, a soil detritivore group, the Archaeognatha, was completely eliminated from both types of vegetation, which could indicate a direct insecticidal effect of the ash on this group of arthropods. In contrast, many of the groups that increased in abundance in the wake of this disruption, including litter microbes, phytophagous nematodes and plant-feeding arthropods of the Homoptera, are more dependent on live or senescent plants as their food source. Weakened plant defence and increased susceptibility to attack the lack of water in the soil matrix (Mattson & Haack 1987; Thomas, Blank & Hartmann 2002) may explain the unexpected increase in this group of phytophagous arthropods. It appears that not only this group is less directly affected by the ash deposition, but predation release, reduction in competition or refuge from detection, could have actually promoted their activity in wake of the volcanic eruption.

On longer time-scales, there may be successional changes in the community of soil biota, and it is possible that the effects observed in this study on litter microbial communities will become more evident for soil properties as pyroclastic deposits are incorporated in the soil profile (Cremona, Ferrari & López 2011). Incorporation of palaeoecological information from the sediment records for previous eruptions would provide further insight into the role of these large-scale disturbances in these Patagonian ecosystems (McLauchlan *et al.* 2014), which can be an important step in placing the role of these large-scale infrequent disturbances in a more robust ecological context.

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## Data accessibility

All data from this manuscript are available in the Dryad Digital Repository: <http://datadryad.org/resource/doi:10.5061/dryad.kf4t9> (Berenstecher *et al.* 2016).

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## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Fig. S1.** Relative abundance (% of total) of orders of ground dwelling arthropods, before and after ash deposition.

**Fig. S2.** Abundance of nematode trophic groups before and after ash deposition.

**Table S1.** Orders of ground dwelling arthropods.

**Table S2.** Absolute abundance of nematode trophic groups.

**Table S3.** Pairwise Pearson correlation matrices between variables evaluated in soil and litter.

**Table S4.** Potential enzyme activities in litter with simulated ash deposition.