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Effects of volcanic ash deposition on the early recovery of gap vegetation in Northwestern Patagonian steppes

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ABSTRACT

Volcanic eruptions can cause changes in plant communities through the effects of ash fall. We studied the effect of ash deposition on vegetation recovery in inter-plant patches (gaps) following the eruption of the Puyehue-Cordón Caulle volcano (June 2011) in the Northwestern Patagonian steppe of Argentina. We estimated the aboveground vegetation cover and the seed bank abundance (April 2012) in gaps with and without ash (November 2011 and December 2012). We compared the sampled data with studies performed in the area before the eruption. Total plant cover was greater in gaps with ash compared to gaps without ash. Ash deposition suppressed cover of therophyte exotic species, but augmented total cover due to the increase of geophyte cover. Pre- and post-eruption soil seed bank was dominated by therophytes, mostly exotic species. However, ash deposition decreased the abundance of the total seed bank, including therophyte species. The position of buds and plant size in relation to ash layer thickness were important in determining plant recovery. Our results indicate that ash derived from volcanic activity can change species abundance and composition of steppe gaps that are important for the regeneration of matrix species.

1. Introduction

Global volcanic activity is an important hazard affecting almost all world biomes. There are 1551 active volcanoes (i.e. Holocene volcanoes), which 868 of them have erupted in historical times (Smithsonian Institution, National Museum Natural History, Global Volcanism Program, 2013). Despite the impacts of volcanic eruptions on many different ecosystems, studies on post-eruption recovery are relatively scarce in steppes (Mack, 1981, 1987; Black and Mack, 1986; Martin et al., 2009; Wilson et al., 2012; Ghermandi and Gonzalez, 2012). However, a high number of active volcanoes impact the arid lands that cover approximately 1/3 of the earth surface. Tephra deposits may cover large regions and their depth varies depending on distance to volcanic source (lower depth at greater distance), but they usually spread homogeneously at a landscape scale (del Moral and Grishin, 1999).

The effects of ash deposition on ecosystems are complex and depend on chemical composition of the ash, size and shape of particles, season of eruption occurrence, depth of ash deposits, type of vegetation and fauna, climate, topography and land use (Dale et al., 2005). Ash alters water use due to plant death and changes water availability because ash texture is different from that of soil particles and produces a mulching effect by retarding water evaporation from soil surface (Black and Mack, 1986), and by increasing water retention because of ash's high porosity (Wilson et al., 2012). Volcanic ash can change the albedo in grasslands (Black and Mack, 1986). An inverse relation exists between soil temperature and albedo, and the gray ash surface has a higher albedo than the darker soil. In open habitats, like the steppe, where seed germination responds positively to soil temperature increases during the growing season (Ferrari and Parera, 2015), the increase of soil albedo can decrease seedling emergence. Ash fall is more detrimental at the start of the growing season (spring) and less severe in autumn, when plants are dormant (Mack, 1981; Hotes et al., 2004).

Initial changes in vegetation cover are greatly influenced by pre-eruption species composition, thus description and monitoring of post-disturbance effects on vegetation soon as eruption is critical (Zobel and Antos, 1997). Complete burial by ash kills small annual species (Smith, 1913; Galán de Mera et al., 1999; Tsuyuzaki and Hase, 2005), but, if the tephra layer is not too deep, plants with buds localized near volcanic ash surface can recover more easily than annual species (Kent et al., 2001; Voronkova et al., 2008). Persistent seed banks can survive under tephra. Mack (1981)

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recorded the seed production of annual species *Draba verna, Holosteum umbellatum* and *Erodium cicutarium* buried after Mount St. Helens eruption and he suggested that these species' recruitment would depend on gaps without ash and that their abundance may be diminished. Ash fall can also have beneficial effects on vegetation, such as reduced seed predation and herbivory by insects due to the insecticide effects of the ash (Buteler et al., 2011; Masciocchi et al., 2012).

Argentinean Patagonia is a vast territory that extends from 37° to 55° S and covers 786,595 km^2 (del Valle, 1998). Most of this region is impacted by eruptions from the Chilean Southern Volcanic Zone (33°–46° S) (Lara et al., 2006; Wilson et al., 2012) which has 500 active volcanoes, 60 of which have historical records during the last 450 years (300 eruptions in total, Servicio Nacional de Geología y Minería de Chile). Dominant winds are westerly and ash fall impacts the steppe that occupies most of Argentinean Patagonia. Recently (1991, 2008) two Chilean volcanoes erupted explosively affecting the Argentinean steppe (Besoain et al., 1997; Lara et al., 2006; Martin et al., 2009). Also the Puyehue-Cordón Caulle volcanic complex erupted on 24 May 1960 following an earthquake (magnitude 9.5, the largest measured earthquake in history) on 22 May. This eruption started with a powerful explosive phase, which formed an ash column 8 km in height (Barrientos, 1994).

In Patagonian steppe, gaps (areas between tussock grasses and shrubs) are the recruitment microsites for dominant plant species (Defossé et al., 1997; Franzese et al., 2009; Franzese and Ghermandi, 2012a,b), and also preserve herbaceous richness (Ghermandi and Gonzalez, 2009). For this reason we studied the early vegetation dynamics of gap microsites after the most recent eruption of the Puyehue-Cordón Caulle volcanic complex. The aims of the present work were to determine:

1) the effect of the volcanic eruption on vegetation cover and on seed bank abundance.
2) the effect of the ash fall on short-term (one season) vegetation recovery and on seed bank recharge (by post eruption seed production).

2. Materials and methods

2.1. Description of the Puyehue-Cordón Caulle volcanic complex and the study area

The Puyehue-Cordón Caulle Volcanic Complex (PCCVC) is located at 40.5° S, 72.2°W in the Southern Volcanic Zone of the Chilean Andes. This complex extends between the Cordillera Nevada caldera (1799 m a.s.l.) and the Puyehue stratovolcano (2236 m a.s.l.) with a fissure system between them named Cordón Caulle (1793 m a.s.l.) (Lara et al., 2006). The PCCVC is one of the most active volcanic complexes in the Southern Andes with eight eruptions occurring in the twentieth century (Lara et al., 2006). The most recent eruption of the volcano complex occurred on June 4, 2011 (SERNAGEONIM, 2014), and according to its high volcanic explosivity index (VEI = 4), it was considered large and infrequent. The volcano complex remained active with decreasing intensity until September 2012, and the emitted ash was distributed by the prevailing western winds beyond the eastern Andes on a vast area of Argentinean Patagonia (Gaitán et al., 2011) (Fig. 1).

Our study was carried out in a semiarid grassland of Northwestern Argentinean Patagonia (30 km E of Bariloche, at the San Ramón ranch; 41°04′S, 70°51′W) located 100 km from the eruption zone. Soil was covered by an average of 3 cm of tephra (Gaitán et al., 2011; Ghermandi and Gonzalez, 2012) (Fig. 1), with particle size ranging from 0.001 to 0.025 mm. To avoid the negative effects of ash fall on livestock, they were temporarily removed from the grassland soon after the eruption. Climate is temperate with a mean annual precipitation of 586 mm (Mediterranean regime with 60% of rainfall accumulated in autumn and winter) and a mean annual temperature of 8.7 °C (San Ramón's Meteorological Station, located 1 km away from the study area). Strong W-NW winds blow frequently throughout the year, accentuating water stress in summer (Godagnone and Bran, 2009). The landscape originated from volcanic activity and presents a relief of smooth plains and hills with numerous rocky outcrops, eroded by the glaciers in the Pleistocene and covered by ash from volcanoes located in Chile during the Holocene (Anchorena et al., 1993; Anchorena and Cingolani, 2002). Dominant soils are moderately developed (Haploxerolls) with sandy-loam texture and superficial horizons containing moderate organic matter (Gaitán et al., 2004). Vegetation cover is approximately 60% and consists of a matrix dominated by the tussock grasses *Pappostipa speciosa* ((Trin. and Rupr.) Romasch, ex *Stipa speciosa*) and *Festuca pallescens* (St. Yves) Parodi, and by scattered mid-sized shrubs such as *Mulinum spinosum* (Cav.) Pers. and *Senecio bracteolatus* Hook etArnott. Gaps (bare areas between tussocks and shrubs) are colonized by small native herbs like *Plagyobothrys verrucosus* (Phil.) Johnst, *Triptilion achilleae* Ruiz et. Pavón, and *Microsteris gracilis* (Hook.), and by exotic herbs like *Draba verna* ((L.) Bess. ex *Erophila verna*), *Holosteum umbellatum* (L.), and *Rumex acetosella* (L.) (Ghermandi and Gonzalez, 2009). Bare soil ranges from 29% to 60%.

2.2. Sampling design

2.2.1. Pre- and post-eruption vegetation and seed bank data

To assess the effect of the volcanic ash deposition on vegetation and soil seed bank, we compared pre- and post-eruption species composition and abundance in gaps. Pre- and post-eruption data sets were collected in the same seasons with similar meteorological conditions (i.e. accumulated precipitation and mean temperature). We collected the post-eruption vegetation data on Nov 2011 (in spring, five months after eruption) from 20 gaps covered by ash ('ash treatment': see detailed sampling in Section 2.2.2). Pre-eruption data were collected in the same study area in Nov 2008 from 50 gaps, where a 0.25 m^2 frame was used to sample the gaps (data published in Franzese and Ghermandi, 2012a).

We collected post-eruption soil samples to evaluate seed bank on April 2012 (in autumn, after seed dispersal and before seed germination) in the same gaps used for vegetation sampling (soil of 'ash treatment': detailed sampling in Section 2.2.2). Pre-eruption seed bank was estimated by the seedling emergence method from soil samples collected in April 2001, in 20 gaps from similar grasslands, and within the same vegetation community, located 3 km away from the current study area in the same paddock (Ghermandi and Gonzalez, 2009). Considering the similarity in plant community, meteorological conditions, and land management during the compared periods, we expected that the observed differences in the analyzed variables are mainly due to the effect of ash deposition.

2.2.2. Ash and ash removal treatments

To assess the short-term effect of ash removal on vegetation recovery and on seed bank recharge, we compared species composition and abundance of vegetation and soil seed bank in gaps with and without ash.

On October 2011 (four months post-eruption), we randomly selected 40 similar-sized gaps (0.46 ± 0.05 m^2) within 1-ha grassland that were assigned to two treatments (n = 20): a) 'ash removal treatment': where we removed the ash using trowels, brushes and a handheld vacuum (minimizing damage to surviving plants), and

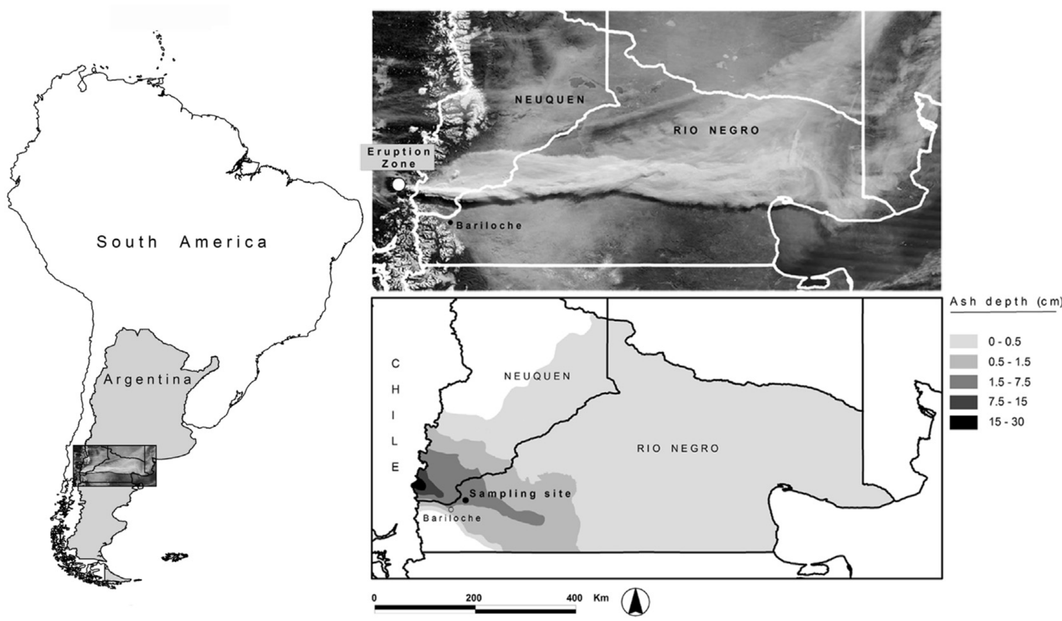

Fig. 1. Río Negro province in Argentina (left), the eruption zone and the ash plume (MODIS-Terra image, 13 Jun 2011; above right), and the sampling site location and the ash deposition depth (modified from Gaitán et al., 2011; below right).

b) 'ash treatment': where we left the ash layer intact. The removal of ash was repeated throughout the study. On Nov 2011 and on Dec 2012 (five and six months post-eruption), we estimated cover of all species in the 'ash' and 'ash removal' treatments using the quadrate method (Mueller-Dombois and Ellenberg, 1974). The quadrate was 1 m^2 and was subdivided into 50 cells. Species cover was estimated considering the area occupied by each species per cell. We assigned a value of species cover per cell (1 when the species occupied completely the cell, and a fraction of 1 when the species partially occupied it). The sum of the cells occupied by the species was divided by the number of cells encompassed by the sampled gap. The value obtained was multiplied by 100 to express cover as a percentage.

On April 2012 (10 months post-eruption), we gathered two 10-cm-diameter soil samples from each one of the 20 gaps assigned to each treatment ('ash' or 'ash removal') (i.e. 2 soil samples $\times$ 20 gaps $\times$ 2 treatments = 80 samples). In the ash removal treatment, samples were collected to a depth of 3 cm. In the ash treatment, we collected two samples: the ash layer (0–3 cm depth), and the soil under the ash (3–6 cm depth). Samples were collected in nylon bags, and stratified for one month in a greenhouse under uncontrolled conditions. After stratification, we sieved the samples to remove organic debris and stones. To determine species composition and estimate seed density of the sample, we used two methods: seedling emergence and seed extraction by salt solution (Gonzalez and Ghermandi, 2012). Each soil sample was divided in halves, each of which was assigned to a method (i.e. seedling emergence or seed extraction method). This estimate represents a sort of intermediate measure of seed density between two alternative methods. For the seedling emergence method, we placed the samples in plastic pots over a sterilized sand layer (100 °C for two days), and kept them in a germination chamber for two months simulating autumn conditions: March, 13 h light (18.1 °C)/11 h dark (4.7 °C); April, 11 h light (13.5 °C)/13 h dark (2.0 °C). Diurnal temperatures for March and April corresponded to the mean maximum monthly temperatures in the study site, while night temperatures were mean minimal temperatures for each month as recommended by Baskin and Baskin (1988). We watered pots daily, and recorded and removed the emerged seedlings weekly. For the seed extraction method, we added the remaining soil samples to a saturated sodium chloride solution which separates the organic matter and seeds from the mineral soil fraction (Gonzalez and Ghermandi, 2012). We manually separated healthy seeds from the organic matter and counted them under a binocular microscope. We determined seed viability by the seed crush test (Borza et al., 2007). Each seed was identified to the genus or species level using seeds collected previously from the study area as a reference catalog.

We classified all the species from the vegetation and seed bank according to the Raunkiaer life forms classification, which is based on the position of growth buds (Raunkiaer, 1934). This classification includes the therophytes, which are annual herbs without perenniating buds; the geophytes, which are perennial plants with belowground buds protected in bulbs, tubers, and rhizomes; the hemicryptophytes, which are plants with buds located at the soil surface (perennial or biannual herbs); the chamaephytes, which have buds near the ground (suffrutescents or low subshrubs); and the phanerophytes, with buds located 25 cm aboveground (trees, shrubs and lianas).

2.3. Data analysis

We used chi-squared analysis to assess whether the proportion of functional groups was similar between pre- and post-eruption conditions in vegetation and in soil seed bank. We compared total vegetation cover between pre- and post-eruption spring data (Nov 2008 *vs.* Nov 2011) using a t-test, and between 'ash' and 'ash removal' treatments (Dec 2012) using a Mann–Whitney test.

For the analysis of soil seed bank data, we averaged the values obtained from the two soil samples in each post-eruption gap, obtaining one mean value per gap (n = 20). Since pre-eruption seed density was estimated only with the seedling emergence method, the comparison with post-eruption seed density (i.e. soil from the ash treatment) was made with data obtained by this method. On the other hand, to compare seed bank composition and density between 'ash treatment' and 'ash removal treatment', we used the data obtained after summing the number of seeds estimated by the seedling emergence and by the seed extraction methods. To compare mean differences in total seed density between pre- and post-eruption data (Apr 2001 *vs.* Apr 2012), between soils of 'ash treatment' and 'ash removal treatment' (Apr 2012), and between soil and ash layers of 'ash treatment' (Apr 2012), we used Generalized Linear Models (GLM) assuming a Negative Binomial distribution, since data showed over-dispersion (glm.nb function, MASS package, R software; Venables and Ripley, 2002). In ash treatment samples, we compared seed abundance between the soil and the ash layer to evaluate post-eruption seed production, and the role of ash as a seed filter that can prevent the incorporation of seeds into soil.

To evaluate species composition similarity between pre- and post-eruption data, and between post-eruption treatments, we used the ordination technique non-metric multidimensional scaling (NMDS), and Analysis of Similarity (ANOSIM). NMDS does not require assumptions about the data and uses the Bray-Curtis coefficient to calculate similarity matrices (Faith et al., 1987). We used ANOSIM to evaluate the significance of differences in species composition (Clarke, 1993). This technique is a non-parametric multivariate analysis of variance that uses a distance matrix and obtains a test statistic R (Clarke, 1993). R values can range between 1 (complete difference in species composition between groups) and −1 (more difference in species composition within groups than between groups). Zero R values indicate no differences in species composition between groups. When the ANOSIM indicated significant differences in composition, we performed a similarity percentage analysis (SIMPER) to assess the identity of the species that made the greatest accumulated contribution to the dissimilarity between the compared data set. These analyses were based on abundance data (vegetation cover or seed bank density), and were performed using the software Primer v6 (Clarke and Gorley, 2006). Significance level for all tests was 0.05.

3. Results

3.1. Vegetation and seed bank comparisons between pre- and post-eruption situations

There were differences in the proportion of functional groups between pre- and post-eruption conditions in both vegetation and soil seed bank (vegetation: $\chi^2 = 18.94$, df = 4, $P < 0.001$; seed bank: $\chi^2 = 14.68$, df = 2, $P < 0.001$). Pre-eruption vegetation was dominated by geophytes, followed by therophytes, hemicryptophytes, with smaller proportions of chamaephytes and phanerophytes (Fig. 2a, Appendix A). Post-eruption, therophytes were absent from vegetation, while geophytes increased their relative cover by19.3% compared to the pre-eruption data. The remaining groups had very low cover values, similarly to what was observed in Nov 2008 (Fig. 2a, Appendix A). The post-eruption seed bank, on the other hand, had the same functional groups as the pre-eruption seed bank, but in slightly different proportions: in Apr 2012 therophyte abundance increased while geophyte abundance decreased (Fig. 2b, Appendix B).

Absolute pre-eruption richness (Nov 2008) was twice as higher as post-eruption richness (Nov 2011) (Appendix A). Absolute richness of the seed bank was also higher in the pre-eruption autumn (Apr 2001) than in the post-eruption sample (Apr 2012) (Appendix B). Total post-eruption vegetation cover of the spring sample was higher than pre-eruption cover (19.1% *vs.* 10.1%, $P < 0.01$), whereas we found the opposite pattern in total seed bank density (179.9 seeds m^{-2}*vs.* 421.8 seeds m^{-2}, likelihood ratio test (LRT) = 9.04, df = 38, $P < 0.026$). The ordination analysis for vegetation and seed bank showed clear differences in species composition between pre-eruption and post-eruption gaps (Fig. 3a,b), indicating that floristic composition was strongly modified by the deposition of ash. The effect of ash was greater on seed bank composition than on vegetation composition, as shown by the ANOSIM analysis (seed bank: Global R = 0.51; vegetation: Global R = 0.27, $P < 0.001$). The species that made a cumulative contribution of 70% to dissimilarity between 'pre-eruption' and 'post-eruption' conditions were almost the same in the vegetation and in the seed bank, but with different individual contribution percentages in each case. Above-ground, cover of the rhizomatous geophytes *Poa lanuginosa* and *R. acetosella* increased and the therophytes *Draba verna* and *Holosteum umbellatum* disappeared after the eruption (Fig. 3c), while, in the seed bank, the latter three species decreased in density (Fig. 3d).

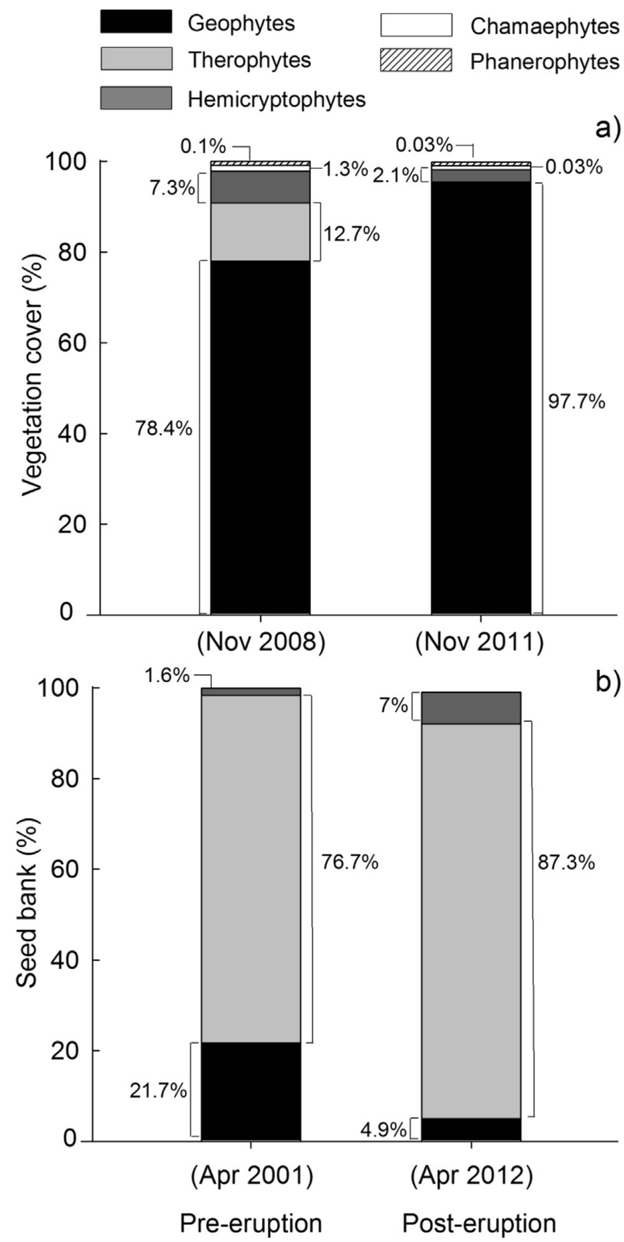

Fig. 2. Proportion of life forms according to the Raunkiaer classification found in (a) the aboveground vegetation in pre- (Nov 2008) and post-eruption (Nov 2011 in 'ash treatment') springs, and (b) the seed bank in pre- (Apr 2001) and post-eruption (Apr 2012 in soil from 'ash treatment') autumn. Soil seed bank was estimated by the seedling emergence method.

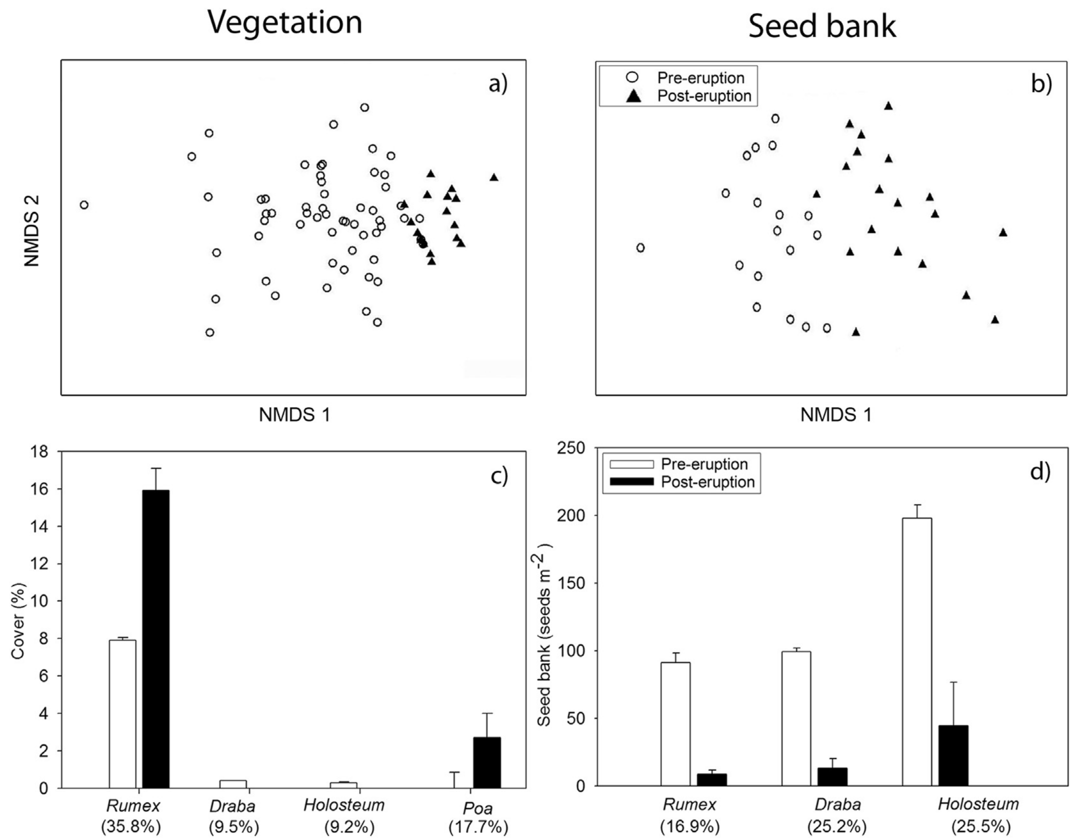

Fig. 3. Two dimensional non-metric multidimensional scaling (NMDS) ordination of (a) vegetation in pre- (Nov 2008) and post-eruption (Nov 2011 in 'ash treatment') springs (stress value = 0.17) and (b) soil seed bank of pre- (Apr 2001) and post-eruption (Apr 2012 in soil from 'ash treatment') in autumn (stress value = 0.18). Ordination based on species abundance data. The location of ordination points within each diagram indicates the degree of similarity. (c) Mean cover (% ± SE) and (d) seed density (seeds m^{-2} ± SE) of the species that made the greatest accumulated contribution (up to 70%) to the dissimilarity between the pre- and post-eruption conditions. We showed in breaks the contribution percentage of each species to the dissimilarity between the compared conditions.

3.2. Vegetation and seed bank comparisons between ash and ash removal treatments

Ordination analysis revealed that species composition of vegetation did not differ between ash and ash removal gaps, a result further confirmed by the ANOSIM (Global R = 0.05, $P > 0.05$, stress value = 0.16). However, there were differences in seed bank composition between the soil of 'ash treatment' and the soil without ash ('ash removal treatment') (Global R = 0.23, $P < 0.001$, stress value = 0.16). The species that contributed most to this difference were (in decreasing order of importance) *D. verna*, *R. acetosella*, and *H. umbellatum*, whose seed bank recharge was particularly affected by the deposition of a volcanic ash layer (Fig. 4a). Consequently, total soil seed bank abundance in the ash treatment (considering only the soil layer) was lower than in the ash removal treatment (ash treatment: 431.8 seeds m^{-2} *vs.* ash removal: 1145.8 seeds m^{-2}, LRT = 16.73, df = 38, $P < 0.0001$).

Although there were significant differences in the seed bank composition between the soil and the ash layer deposited on it, they were not pronounced (Global R = 0.21; $P < 0.001$, stress value = 0.13). Accordingly, the ordination analysis showed a considerable overlapping of soil samples with the ash layer samples. Compared to soil, the ash layer had lower seed density of *D. verna*, and greater density of *R. acetosella* and the hemicryptophyte *F. pallescens* (Fig. 4b). Soil samples contained greater seed density than ash samples (LRT = 6.11, df = 38, $P < 0.013$). The ash layer retained 82.2 seeds m^{-2}, a quantity that represented almost half of the seeds contained in the soil (179.6 seed m^{-2}).

4. Discussion

In our study, the most conspicuous effects of ash deposition on aboveground vegetation were the disappearance of therophyte species, the decrease of species richness and the increase of total cover. In gaps with ash, the cover of *R. acetosella* was two-fold greater than in the pre-eruption spring gaps. *R. acetosella* is an exotic geophyte herb, introduced in Patagonia to the early 16th century (Huber and Markgraf, 2003). Other species that responded positively to ash were *P. lanuginosa*, a rhizomatous native grass, and the native hemicrypthophyte herb *Galium richardianum.* A possible explanation for the increase in cover of these perennial species could be the increased soil water retention of volcanic ash (mulching effect, Cremona et al., 2011) which does not rule out the possibility that the finer ash fraction (size range between 0.001 and 0.025 mm) could have released some nutrients that acted like a fertilizer (Cremona et al., 2011). This effect is probably very short-lived because ash can loses nutrients rapidly (Zobel and Antos, 1991).

The main effect of explosive volcanic eruptions on vegetation is ash deposition, which produces different degrees of plant burial depending on thickness of the ash layer. The damage depends also on grain size of ash and season of disturbance (Mack, 1981; Hotes et al., 2004). Understory recovery of forest after tephra burial has been studied in Japan and authors found that the topsoil contributed to revegetation by the seed bank and that small herbaceous species died because they were completely buried (Tsuyuzaki and Hase, 2005, Tsuyuzaki, 2009). Perennial species (herbs and shrubs) were dominant because of clonal development due to the

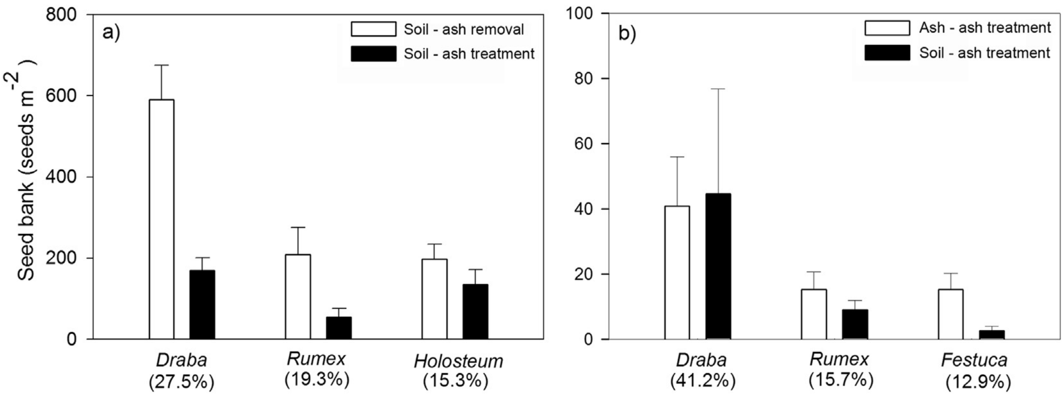

Fig. 4. Seed density (seeds $m^{-2} \pm$ SE) of the species that made the greatest cumulative contribution (70%) to the dissimilarity between (a) soils from "ash" and "ash removal" treatments (Apr 2012) and between (b) soil and ash layers from "ash treatment" (Apr 2012). We showed in breaks the contribution percentage of each species to the dissimilarity between the compared conditions.

presence of underground organs that facilitated rapid recovery (Tsuyuzaki, 1994; Kent et al., 2001).

The position of growth buds and plant size relative to ash layer thickness is very important to post-eruption plant recovery. Our results support this concept since gap vegetation responded with a high recovery from the geophyte group and with the disappearance of the small therophytes. These species did not become extinct locally: we have recorded them in autumn 2013, recruited from fossorial rodent removal mounds. The activity of burrowing animals ensures faster recycling of buried soil containing viable long-lived seeds (Dale et al., 2005). Seeds of therophytes species form a persistent seed bank (Ghermandi, 1997) and soil removal allows buried seeds to reach the surface, even after ash fall. In the ash layer, we also found seeds of species that dominate the grassland matrix (*P. speciosa* and *F. pallescens*). Dominant tussock grasses produced seeds during the first growing season after the eruption (Ghermandi, pers, obs.) and the ash layer could function as a filter that selectively retains larger seeds. Gaps constitute a safe site for the matrix species such as the perennial grasses (Franzese and Ghermandi, 2012b) where they could germinate.

It is not easy to explain the reason for the difference in total seed amount between the gaps where ash was removed and the remaining treatments. The greatest contribution to the seed bank was by *D. verna* (80% in gaps with and without ash), and this species was not found in the aboveground gap vegetation. One possibility to explain the differences in seed number between treatments is that the presence of ash could induce secondary dormancy in *D. verna* seeds. The quality and quantity of light passing through the topsoil layers could be modified, and this effect may induce dormancy in species that detect gaps throughout the light quality (Baskin and Baskin, 1988). Another possibility is that the albedo modification could change the soil's thermal regime, preventing *D. verna* germination.

The effect on grassland gap vegetation of the deposition of a finely textured 3-cm deep ash layer differed greatly to the effect of fire. In fact, in the case of the ash deposition, species richness declined due to the disappearance of annual species, while after grassland wildfires, a pool of native fugitive species temporarily appears in the aboveground vegetation, leaving many seeds in the seed bank (Ghermandi et al., 2004, 2013). In spite of this difference, a species that was favored by both disturbances is *R. acetosella*. It is possible to suppose that in the absence of this invasive species and domestic livestock (the introduction and dispersion of *Rumex* in the Patagonian region was associated with livestock; Huber and Markgraf, 2003), ash accumulation would have favored rhizomatous native species such as the grass *P. lanuginosa*, which has a high forage value.

The occurrence of fires and volcanic eruptions (frequent events at different spatial scales in the Patagonia region) causes complex dynamics, along with other large scale disturbances as grazing, climatic oscillations (including ENSO), and changes in land use (e.g. forestry, stockbreeding), which assist in maintaining the current species pool of the grasslands. However, the grassland condition is vulnerable to an excessive land use by humans (e.g. overgrazing), especially if the use overlaps with disturbances like fires or volcanic eruptions that have a high potential of producing changes in the ecosystem. Also, the time of the year in which these disturbances occur is important. While fires are generally concentrated in the summer (January–February, Oddi, 2013), ash fall can occur at any time of the year. A spring eruption could be potentially more harmful to vegetation than dormant-season eruptions, such as the eruption studied in this work, which occurred in late autumn.

5. Conclusions

The position of buds and plant size in relation to ash layer thickness were important in determining plant recovery in NW Patagonian grasslands. While volcanic ash deposition allowed an increase in the cover of geophytes (especially the native, palatable grass *Poa lanuginosa*), it caused the temporary disappearance of all therophyte (annual) species.

In the Southern Hemisphere, volcanic activity along with other disturbances as fire and grazing is an important driver of ecosystem changes. Volcanic activity has been frequent in the region since the Andes rose (Ramos, 1999). In the study area both, volcanic ash depositions and big wildfires, affect vegetation dynamics at landscape scale (Ghermandi et al., 2004; Ghermandi and Gonzalez, 2012). In the area of ecological studies, we consider that the most important difference between volcanic eruptions and fire is that in many regions of the world, volcanic eruptions are infrequent or absent, making it difficult to develop "volcanic ecology" as has occurred with fire ecology. Swanson and Major (2005) said that Mount St. Helens erupted about 20 times in the past 4000 years and they opined that, across that region and over an evolutionary time scale, climate and biota interacted with disturbances like fire, grazing, drought and volcanism. This situation is similar to that found in Chilean and Argentinean Patagonia, where volcanic activity is much more frequent than in the region of Mount St. Helens. Therefore, this disturbance regime together with fire and grazing regimes could have driven the evolution of vegetation in Patagonia.

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Appendix A. Supplementary data

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