Simon *et al. Fire Ecology* (2025) 21:13
https://doi.org/10.1186/s42408-025-00354-7

Fire Ecology

ORIGINAL RESEARCH

Open Access

Soil redistribution and seed availability after fire events in mixed *Austrocedrus chilensis* forests in Northern Patagonia (Argentina)

Alois Simon[1], Paola Bravo Almeida[2,3], Clemens Geitner[2], María Melisa Rago[4,5], María Florencia Urretavizcaya[4,5], Helge Walentowski[1*] and Stefan Zerbe[3,6]

Abstract

Background Severe wildfires in forest ecosystems promote soil erosion and the loss of fertile soil as a scarce natural resource. Our objective was to quantify post-fire ecosystem response in terms of soil accumulation and seed availability through redistribution. Within our study area in Northern Patagonia, Argentina, we chose three study sites at which forest fire events occurred in different years, namely 1 year post-fire (2022), 2 years post-fire (2021), and 8 years post-fire (2015). At each of the sites, we recorded both burned and control slope transects. Along these transects, three accumulation zones were differentiated, at each zone the amount of accumulated soil material as well as the number of seeds in it were determined.

Results We observed significant amounts of accumulated soil material along the slopes with the highest annual rates in the first year after the forest fire. The mean accumulated soil material (± standard deviation) over all slope accumulation zones increased from 9.5 ± 2.6, 15.9 ± 4.6 to 42.9 ± 14.0 kg*m^{-2}, at the 1 year-old, 2 years-old, and 8 years-old forest fires sites. Despite the generally high spatio-temporal variability of seed dispersal, the transects at the burned forest sites show significantly lower numbers of seeds than control transects. In the investigated burned forest sites, the total number of seeds of the four tree species found was 64, 250, and 252 seeds*m^{-2} in the 1 year-old, 2 years-old, and 8 years-old site, respectively. In general, the more recent fire events had lower number of seeds, which increased with accumulated soil material and time. We also observed a greater number of shrub seeds in the burned sites, but these did not show a pattern with time since the wildfire events.

Conclusion Among the 14 species recorded, the tree *Austrocedrus chilensis* and the shrub *Aristotelia chilensis* emerge as key players in post-fire recovery, with the highest number of seeds at all study locations. Forest restoration after disturbance is a global challenge, especially in the context of large-scale forest fires. Understanding the risk of soil redistribution and seed availability will assist restoration efforts and ecosystem management.

Keywords Forest wildfire, Forest recovery, Post-fire forest management, Soil erosion, Native and non-native species, Seed bank, Slope transects

*Correspondence:
Helge Walentowski
helge.walentowski@hawk.de
Full list of author information is available at the end of the article

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Resumen

Antecedentes Los fuegos severos en ecosistemas forestales promueven la erosión del suelo y la pérdida del suelo fértil, el cual es un recurso natural escaso. Nuestro objetivo fue cuantificar las respuestas post-fuego del ecosistema en términos de la acumulación del suelo y la evaluación de la redistribución de semillas de árboles, arbustos y hierbas identificables. Dentro de nuestra área de estudios en el norte de la Patagonia, Argentina, elegimos tres sitios en los cuales los eventos de incendio habían ocurrido en diferentes años (2022, 2021, y 2015), es decir muestreamos 1, 2, y 8 años después de ocurrido los incendios. En cada uno de los sitios, establecimos transectas en laderas quemadas y no quemadas. A lo largo de las transectas diferenciamos tres zonas de acumulación, y en cada zona se determinó la cantidad de material de suelo acumulado y el número de semillas en el misma.

Resultados Observamos una cantidad significativa de material de suelo acumulado a lo largo de las laderas con la mayor tasa de acumulación en el primer año luego del evento de incendio. La cantidad de material de suelo promedio acumulado (± un error estándar) sobre todas las áreas de acumulación de las laderas se incrementó de 9.5 ± 2.6, 15.9 ± 4.6 a 42.9 ± 14.0 kg*m^{-2}, en los años 1, 2, y 8 luego de los eventos de fuego. A pesar de la alta variabilidad en la dispersión espacio-temporal de las semillas, las transectas en las áreas quemadas mostraron un número significativamente menor que en las transectas control. En los sitios quemados investigados, el número total de semillas de las cuatro especies de árboles encontradas fue de 64, 250, and 252 semillas*m^{-2} en los sitios quemados 1, 2, y 8 años antes, respectivamente. En general, los eventos de fuego más recientes tuvieron un menor número de semillas, que fue aumentando en el tiempo con incrementos en la acumulación del material del suelo. Observamos un gran número de semillas de arbustos en las áreas quemadas, aunque no mostraron un patrón relacionado con el tiempo desde la ocurrencia de los eventos de fuego.

Conclusiones Entre las 14 especies registradas, el árbol *Austrocedrus chilensis* y el arbusto *Aristotelia chilensis* emergieron como las especies clave en la recuperación post-fuego, con el mayor número de semillas en todos los sitios de estudio. La restauración de bosques luego de un disturbio es un desafío global, especialmente en el contexto de incendios forestales de gran escala. El entendimiento del riesgo que implica la redistribución del suelo y la disponibilidad de las semillas ayudará en los esfuerzos de restauración y manejo de ecosistemas.

Introduction

Wildfires have always been a part of global ecosystems and influence their patterns and processes (Bowman et al. 2009). However, their impacts on ecosystems and consequently on human societies must also be considered an environmental problem of global significance (Moritz et al. 2014; Jones et al. 2022; Ruggirello et al. 2023). Most wildfires around the world are anthropogenically initiated rather than occurring as naturally ignited wildfires (Nagy et al. 2018; Cattau et al. 2020). The ecosystem response to severe wildfires (Keeley 2009) can have huge negative impacts on natural ecosystems, land-use systems, biodiversity, ecosystem services, and human health and welfare (Giorgis et al. 2021; Akdis and Nadeau 2022; Roces-Díaz et al. 2022).

The effect of fire on soils includes loss of the organic humus layer, changes in soil structure, increased hydrophobicity, reduced carbon and nutrient pools and fluxes, and altered composition and activity of soil biota (McLauchlan et al. 2020). Additionally, large-scale fires promote soil erosion and thus the loss of fertile soil as a scarce natural resource (Depountis et al. 2020; Vieira et al. 2023). Sartori et al. (2019) estimate the mean annual global soil erosion rate on arable land to be more than 11 t*ha^{-1}, particularly in countries of tropical and subtropical climate zones. However, soil erosion following wildfires is becoming increasingly important (Agbeshie et al. 2022) but is often not included in current estimates of soil erosion under climate change projections, including the study by Riquetti et al. (2023) for South America. When the effects of fire and soil erosion combine, this can lead to substantial and irreversible land degradation, aridization, and even desertification. After severe forest fires, water runoff is increased, thus accelerating soil erosion processes (cp. Evelpidou et al. (2022)). Additionally, the loss of vegetation and litter layers reduces the ability to intercept rainfall (Larsen et al. 2009), leaving the soil much more exposed to direct raindrop impact. The reduction of water infiltration (César 1989) is often also favored by the development of a heat-induced hydrophobic layer below the soil surface (Morales et al. 2013) which significantly affects soil-related surface runoff conditions and thus may alter the water balance and productivity of the forest stand in a long term (Pellegrini et al. 2018). Taking into account the manifold soil-based ecosystem services, this additive or interactive effect of wildfires has additional impacts on biodiversity, carbon stocks,



Fig. 1 Former forest area of mixed *Nothofagus-Austrocedrus* forests and shrubland at the Lago Steffen study area (see Table 1, Fig. 2) destroyed by a fire in 2022 (photo by Alois Simon)

and climate change as well as the landscape water balance.

As a result of ecosystem response to fire, tree and forest regeneration is slowed down (Prestes et al. 2020; Mantero et al. 2023) or interrupted by the loss of seed-bearing trees and the reduction of the soil seed bank (Duivenvoorden et al. 2024). Besides, there may be a redistribution of seeds with soil material, since many factors influence the horizontal and vertical movement of seeds, such as the intensity of wind and precipitation on the soil surface, several soil properties, and the vegetation that acts as sites of seed retention, are modified after fire (Chambers and MacMahon 1994). The input of new seeds in the burned areas may depend on seed biotic and abiotic dispersion from surrounding unburned areas and from resprouting species that provide seeds to the soil seed bank, regardless of the distance to the edge of the remnant's forest (Falk et al. 2022).

In Patagonia in the southern part of South America, rare wildfires were ignited naturally by lightning before major human impacts at the landscape level (Veblen et al. 2003). The vast majority of forest fires in the region were and are undoubtedly caused by humans. According to Seibert (1979), only 10% are of natural origin (lightning). Today, it is evident that both, direct human impact (e.g., opening the forest pastures) as well as climate change have dramatically increased the occurrence and expansion of forest fires since the mid-1800s (Kitzberger and Veblen 1997, 1999). Veblen et al. (2008), for example, recorded several fire events with high severity that occurred in the *Nothofagus* forest region of southern Argentina and Chile from the 1980s to the early 2000s. In the last 20 years, fire has burned very extensive areas, affecting more than 100,000 ha only in Chubut Province, most of which were burned in the fires that occurred in 2015 and 2021 (SSB et al. 2015; SSB and CIEFAP, 2022). Warm summers coincide with enhanced lightning activity, further influencing the fire dynamics in the region (Veblen et al. 2003). Most fires in Patagonia (> 90%) occur during the warm and dry season from October to March, which is the southern hemispheric summer season, and have continued to destroy large areas of native forest in recent decades (Fig. 1).

The different tree and shrub species in the Patagonian forests exhibit varying levels of resistance to and recovery from fire. For example, the dominant tree species in this study, *Austrocedrus chilensis* ((D. Don) Pic.-Ser. & Bizz.) (hereafter abbreviated as *A. chilensis*, in contrast to the shrub species *Aristotelia chilensis* (Molina) Stuntz), can only resist fire in later life stages. The relatively thin bark of young specimens makes them vulnerable to fire-induced mortality (Urretavizcaya and Defosse 2019) and cannot reproduce vegetatively. Another key characteristic of *A. chilensis* is its wind-mediated seed dispersal favored by small, unequally bi-winged seeds (Vidaković, 1991), with most seeds falling within a short distance of the mother plant, but capable of dispersal over 400 m (Landesmann and Morales 2018). However, the viability of *A. chilensis* seeds in the soil does not exceed beyond 1 year and there is a high annual variability in seed production (Urretavizcaya and Defosse 2004). The second main tree species, *Nothofagus dombeyi* ((Mirb.) Oerst.),

also does not regenerate vegetatively by adventitious shoots or suckers and mature trees have only a low fire resistance. Therefore, they have to rely on regenerative recruitment from seeds after fire (Urretavizcaya and Defosse 2004; Landesmann and Morales 2018) or moderate-intensity topsoil disturbance (Zerbe et al. 2023). On the contrary, *Nothofagus antarctica* ((G. Forst.) Oerst.) mainly reproduces asexually from lignotubers and basal buds. Many predominant shrubs of Patagonia also have the capability of resprouting after fire from buried structures. But some of them also rely on seeds resistant to fire (Ghermandi et al. 2013) or on seed dispersion, for example, birds play a fundamental role during early post-fire revegetation (Cavallero et al. 2013).

In our study, we focused on the extent of post-fire disturbances and recovery in native *A. chilensis* forests mixed with species of the genus *Nothofagus*, specifically regarding soil redistribution and seed availability, which is only weakly understood so far. We therefore quantify soil accumulation and evaluate the redistribution of seeds from trees but also from shrubs and identifiable herb species. From our findings, we derive recommendations for post-fire forest management and restoration. Restoring forests after fires will be a challenge for the future of Patagonian forests and the multiple ecosystem functions and services they provide.

Materials and methods

Study area and sample sites

The study was performed in north west Patagonia (Argentina) in the provinces of Chubut and Rio Negro from November to December 2022 and was carried out at the eastern slopes of the Andes at around 700 m asl (Fig. 2, Table 1). The study system is covered with native forest vegetation of the spure *A. chilensis* forest mixed with individuals of *N. dombeyi* (Figs. 1 and 2). In post-disturbance forest stands, *N. antarctica*, *Lomatia hirsuta* (Diels ex J.F. Macbr.), *Maytenus boaria* (Molina), and *Embothrium coccineum* (J.R. Forst. & G.Forst.) can be part of the tree species composition (Seibert 1979; Orellana and Novella 2018). However, with advanced forest development and in the absence of disturbances, these species play only a minor role, except for drought-prone sites. In addition to the native tree species, plantations of non-native conifers were established in the study region (CIEFAP and MAyDS, 2016), which are known to have invasive characteristics (Sarasola et al. 2006; Orellana and Raffaele 2010).

The eastern slopes of the Andes face a very pronounced precipitation gradient, with a sharply declining mean annual precipitation (MAP) from west (appr. 2.000 mm) to east (appr. 500 mm) (Karger et al. 2017), i.e., from the Cordillera to the Patagonian steppe. The soils are mainly Andosols of volcanic origin (IUSS Working Group WRB 2014; Buduba et al. 2020; Serna et al. 2020), and are, in general, characterized by a high cation exchange capacity, low to moderate base saturation, a high-water storage capacity, and naturally moderate nitrogen contents (Kühn et al. 2021). One of the strongest limitations for plant growth on allophanic andosols is the low phosphorus availability (Matsuoka-Uno et al. 2022).

Within our study area, three study sites with high fire severity (crown fire) were chosen (Fig. 2) at which forest

Table 1 Characteristics of the three sampling sites at the eastern slopes of the Patagonian Andes (cp. Fig. 1) with different years of fire events. Abbreviation of sample locations at the sites: Mb/Mc, Sb/Sc, Gb/Gc, Rb/Rc, Cb/Cc, Hb/Hc, where b stands for burnt and c for control; Aspect: orientation of slope

Sites	**Lago Steffen**		**Piltriquitrón mountain range**		**Cholila**	
Locations and transects	Mb—burned Mc—control	Sb—burned Sc—control	Gb—burned Gc—control	Rb—burned Rc—control	Cb—burned Cc—control	Hb—burned Hc—control
Coordinates	−41.53853° −71.51478°	−41.54087° −71.51712°	−42.09482° −71.43060°	41.90968° −71.48614°	−42.44158° −71.62245°	−42.44453° −71.64681°
Elevation asl	681 m	620 m	706 m	701 m	706 m	624 m
Aspect	South-west	South	South	South-west	South	South
Average slope	24°	25°	24°	33°	28°	28°
Initial forest type	*A. chilensis* with *N. dombeyi*	*A. chilensis* with *N. dombeyi*	*A. chilensis* with *N. dombeyi*	*A. chilensis* with *N. dombeyi*	*A. chilensis* with *N. antarctica*	*A. chilensis*
Age of fire event (year)	1 year post-fire (2022)		2 years post-fire (2021)		8 years post-fire (2015)	
Period of fire	December 2021 to April 2022		January to March		Mid-February to mid-April	
Forest area affected by the fire	8363 ha		17,300 ha (11,000 ha native forest)		28,000 ha	
Reference	Kitzberger et al. (2023)		(Mohr-Bell 2021a, 2021b)		(Zacconi 2015)	

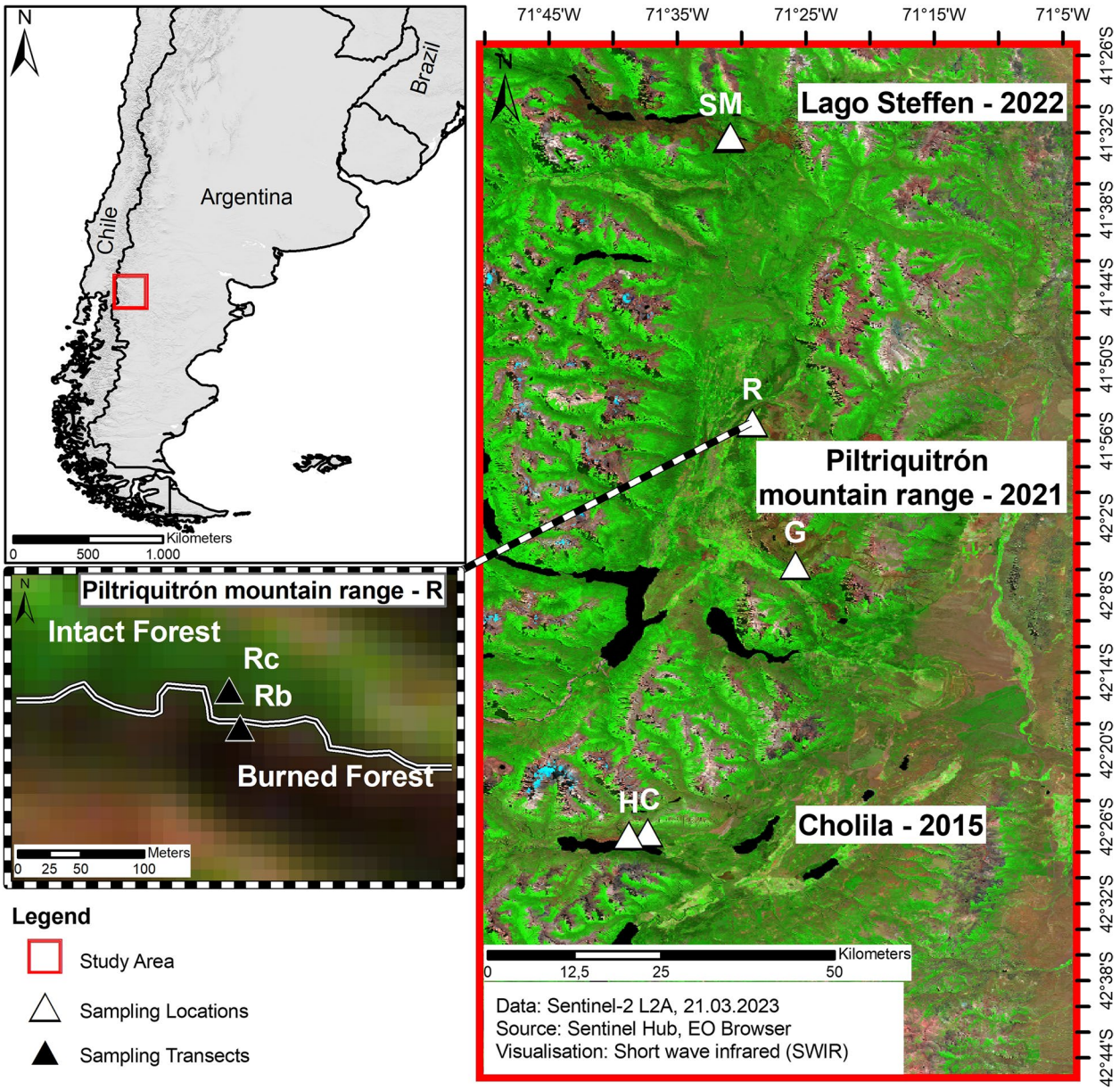


Fig. 2 Study area in Northern Patagonia (Argentina) with three post-fire sampling sites each with two sampling locations (M/S, G/R, C/H) and burned (b) and control (c) sampling transects (example for Piltriquitrón mountain range—R sampling location at the lower left panel). For further description of the sampling locations see also Table 1

fire events occurred in different years, namely 8 years ago (2015), 2 years ago (2021), and 1 year ago (2022) (Table 1). To visualize the forest fire area at the sampling locations (Fig. 2, lower left panel), we used the Short Wave Infrared (SWIR) composite (B12, B8A, B04) of Sentinel-2 satellite data, which proved to be suitable for burned area detection (van Dijk et al., 2021), processed by the Sentinel Hub, EO Browser. Common characteristics of the sampling locations are south-facing slopes and an elevational range between 620 and 720 m asl.

Sampling design

At each of the three study sites, two locations were selected. At each location, one slope transect in the intact forests, not affected by the recent fire as control plots, and three slope transects in the burned forest were sampled (Fig. 2). The respective sampling design with the control (c) and burned (b) sampling transects and photographs of the burned sites are shown in Fig. 3. The selected slopes at the sample locations had a length between 100 and 200 m and were first divided into areas of erosion and

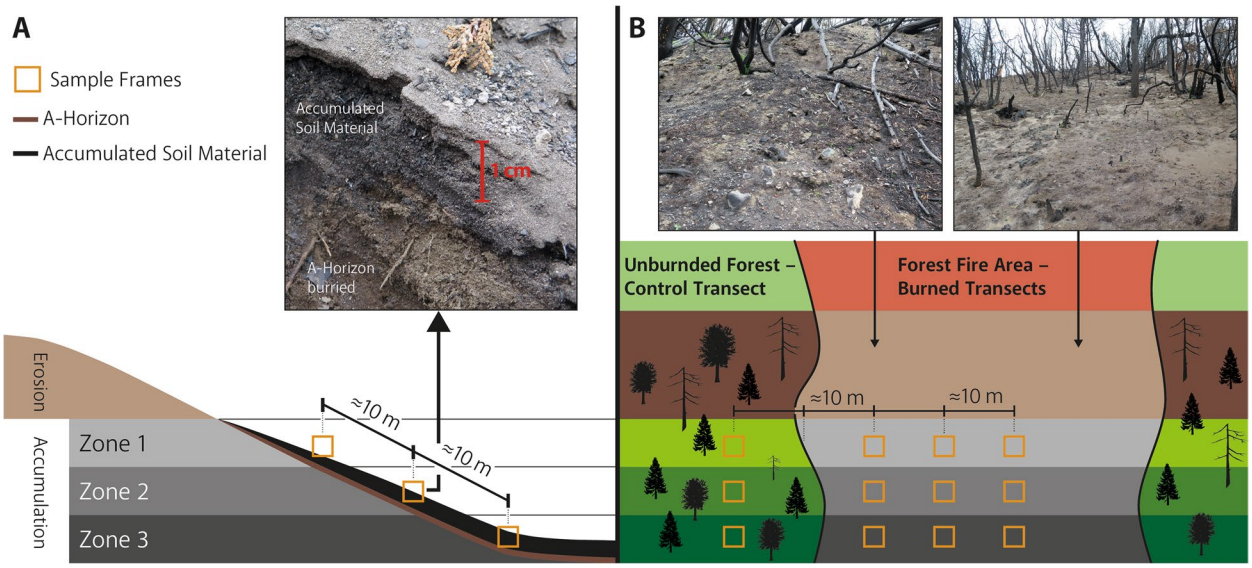


Fig. 3 Sampling design at the three study sites in the intact forest (control) and at the burned forest. **A** Profile view (left panel); **B** plan view (right panel)

accumulation of soil material. As the chosen retrospective sampling method does not allow the detection of erosion, only the area of the slope with accumulation of soil material was sampled. Therefore, this part was further subdivided into three different accumulation zones, namely zone 1 as an incipient zone of accumulation at the backslope position, zone 2 as an intermediate accumulation zone at the transition from the backslope to the footslope position, and zone 3 as an increasing accumulation zone at the footslope to toeslope position (Fig. 3A, slope positions according to IUSS Working Group WRB (2014)). Within a transect, undisturbed samples were taken at the three accumulation zones, each with an iron frame of 20 cm × 15 cm, representing 0.03 m^2, to a soil depth of 10 cm. The transect at the burned forest started approximately 10 m away from the first surviving trees with three replications. We estimated that 10 m is the average canopy height of the intact forest and that most of the seeds of the tree species studied are dispersed within the distance (10–30 m) of the three sampling transects. In parallel, the control transect was located 10 m away from the forest edge within the intact forest. Accordingly, a total of 54 samples were taken at the burned and 18 samples at the control transects.

Analyses of soil accumulation and seed availability

The undisturbed samples within the sampling frames were taken to the laboratory to separate the newly accumulated soil material deposited above the burned former topsoil horizon. The picture in Fig. 3A gives an impression of the accumulated soil material, the burned former topsoil and the buried A-horizon. The boundary between the two layers was still visible at all ages since the fire event and the separation was made carefully from top to bottom using a spatula and a brush. Only the accumulated soil was considered for the analyses and the soil material exceeding the 10 cm sampling depth (relictic topsoil) was discarded. In the case of the samples from the 8 years-old forest fire sites, the thickness of the deposited material exceeded the sampling depth of 10 cm. Therefore, it was not possible to quantify the total deposited material, but at least the minimum deposited soil material. For the samples of the control transects in the intact forests, soil material was taken up to a depth of 5 cm. We assumed that seeds only penetrate to very shallow depths in undisturbed topsoil and that most of the seeds for revegetation are located in this layer (Wolters and Bakker 2002). All soil samples were dried at 80 °C for 24 h and the oven dry weight was determined.

Afterward, the samples were sieved with a 4-deck sieve with 5.0 mm, 3.0 mm, 2.0 mm, and 1.4 mm mesh sizes to separate seeds from the soil material. The material of the size class between 1.4 and 2 mm has been thoroughly checked for the occurrence of small-seeded species (Price et al. 2010). Seeds were then separated from the sieved material with a magnifying glass or under the microscope and sorted according to size, shape, and color. Undamaged seeds were counted and identified using the "Active Seed Bank of the Terrestrial Ecosystem Ecology Area of CIEFAP" (Banco Activo de Semillas del Área de Ecología de Ecosistemas Terrestres del CIEFAP)

and specific literature (Correa 1969). For the analysis, all the undamaged seeds were used (Table 3).

The R statistic software (R Core Team 2019) was used to perform the statistical analysis and the graphical output. We tested the data for normal distribution with the Shapiro–Wilk test and interpretation of normal qq-plots. Possible data transformations were assessed using the R package "bestNormalize" (Peterson 2021) and, where necessary, a logarithmic scale was used to obtain a normal distribution. For normal distributed data, we used the t-Test from the R package "stats" (R Core Team 2019). For non-normal distributed data, the Kruskal–Wallis-Tests with posthoc Nemenyi-Tests (method = Tukey) from the R package: "PMCMR" were used (Pohlert 2014). The variables used in the ordinary least squares (OLS) linear regression and the subsequent ANOVA test were accumulation zones (1, 2, 3), slope inclination, age of forest-fire event, forest type, namely *A. chilensis*, *A. chilensis-N. dombeyi*, and *A. chilensis-N. antarctica*, aspect of the slope (south and southwest), mean annual precipitation, and the individual study sites (Table 1). A Poisson distribution and a Gaussian distribution with data transformation have been tested for modeling of seed availability. A "paired *t*-test" analysis was performed to compare the means of the number of seeds present in the burned and control transects. For graphical display, the R packages "lattice" (Sarkar 2008) and "tactile" (Larsson 2022) were used.

Results

Soil accumulation

The amount of deposited soil material at the different accumulation zones of the burned forest transects is shown in Fig. 4. We observed a clear trend regarding the time elapsed since the forest fire (age), with increasing soil accumulation over time but with a decreasing annual accumulation rate. Mean soil accumulation over all accumulation zones sampled (± standard deviation) was 9.5 ± 2.6 at the 1 year-old (b-1), 15.9 ± 4.6 at the 2 years-old (b-2), and 42.9 ± 14.0 kg*m^{-2} at the 8 years-old (b-8) post-fire sampling locations. Accordingly, the mean annual accumulation rate was 9.5 ± 2.6 (b-1), 7.9 ± 2.3 (b-2), and 5.4 ± 1.8 (b-8) kg*m^{-2}*year^{-1}. The more recent fire events indicate an increase in deposition from zone 1 to zone 3 along the slopes. The sampling locations of the 2022 fire event (Mb, Sb), in which at the time of sampling approximately 1 year has passed since the forest fire, showed an average accumulation thickness of around 1–2 cm and the locations of the 2-year-old fire event (Gb, Rb), 2–4 cm.

The OLS linear regression (Table 2) showed that the age of the fire event has a highly significant influence (p value < 0.001), followed by aspect, and by accumulation zone with a significant influence (p value < 0.05). The variables used for predicting the amount of accumulated soil material explained 82.4% (adjusted R^2) of the variance (Table 2).

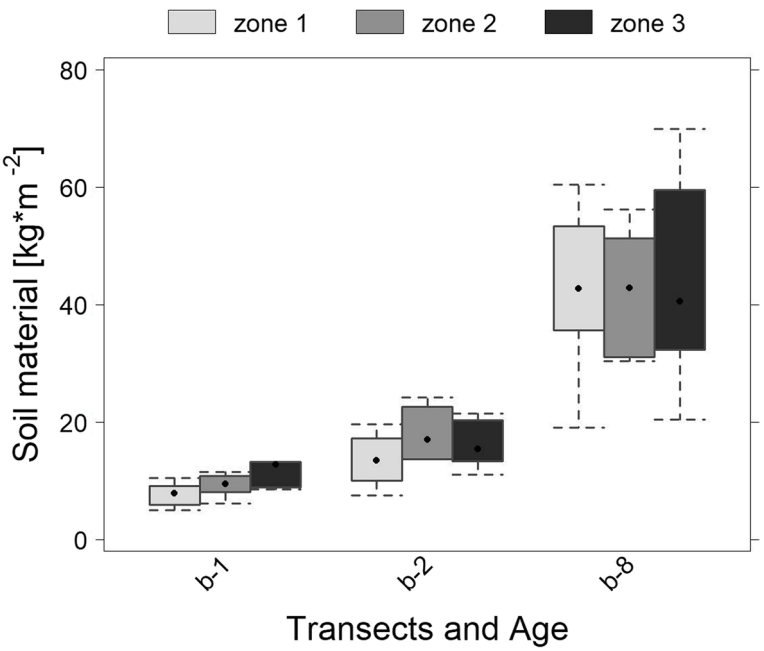


Fig. 4 Accumulated soil material after forest fire of different ages related to the accumulation zone. Fire events b-1 (2022), b-2 (2021), b-8 (2015); points: median values; whiskers = 1.5*interquartile range

Table 2 Results of the OLS linear regression for the amount of accumulated soil at the burned transects as response variable

Predictor variables	Estimate	Standard error	Significance
Intercept	2.169	0.100	< 0.0001
Age 2 (2021); compared to age 1 (2022)	0.511	0.097	< 0.0001
Age 8 (2015); compared to age 1 (2022)	1.616	0.108	< 0.0001
Accumulation zone 2; compared to zone 3	− 0.036	0.009	0.7060
Accumulation zone 1; compared to zone 3	− 0.215	0.009	0.0310
Aspect southwest; compared to aspect south	0.258	0.009	0.0100

Model results: *F*-statistic (df = 48) 50.87, $p < 0.0001$; multiple $R^2 = 0.841$, adj. $R^2 = 0.824$. Model: lm(accumulated soil material ~ accumulation zone + factor(age) + aspect); tested but not significant or highly intercorrelated variables are slope inclination [°]; study site; mean annual precipitation [mm] from global downscaled climate data with a resolution of appr. 1 km (Karger et al. 2017); forest type

Seed availability

We counted a total of 2837 undamaged seeds. Among them, we could identify 13 species, and only 2.6% of the seeds remained unidentifiable (Table 3). We found seeds from the tree species *N. antarctica*, *N. dombeyi*, *A. chilensis*, *M. boaria*, and *P. ponderosa* (Lawson & Lawson); from the shrub species *Schinus patagonica*, *Ovidia andina* (Poepp. & Endl.) Meissn., *Aristotelia chilensis*, *Berberis* spp., *Discaria chacaye* (Don) Tortosa, and *Diostea juncea* (Gill. & Hook.) Miers; and from the herb species *Alstroemeria aurea* (Graham) and *Vicia nigricans* (Hook. & Arn.). Furthermore, we identified fruits of *Muehlenbeckia hastulata* (J.E. Sm.) I.M.Johnst. in the sampled soil material. Seeds from *A. chilensis*, among trees, and from *Aristotelia chilensis*, among shrubs, predominated in all the study sites and locations. In the investigated burned forest sites, the abundance of tree seeds (Table 3) found were 64, 252, and 250 seeds*m^{-2} in Lago Steffen (1 year-old), Piltriquitrón mountain range (2 years-old), and Cholila (8 years-old), respectively. This shows that the most recent fire event had the lowest number of tree seeds, and that the presence of seeds in older sites (2 and 8 years) may not depend on the age of the wildfire anymore. At the control transect, we found 1787, 1789, and 934 tree seeds*m^{-2} in Lago Steffen (1 year-old), Piltriquitrón mountain range (2 years-old), and Cholila (8 years-old), respectively. The number of shrub seeds was greater than tree seeds both in the burned and unburned forests. In the burned forests, we found 574, 260, and 818 seeds*m^{-2} in the 1 year-old, 2 years-old, and in 8 years-old site, respectively. In the unburned (control) forests, we found 1350, 789, and 1711 seeds*m^{-2} in the 1 year-old, 2 years-old, and in 8 years-old sites, respectively.

Figure 5 shows the total number of seeds found in the sampled transects. The transects in the burned forest sites (650 ± 717; 557 ± 468; 1150 ± 967 seeds*m^{-2} (mean ± standard deviation) for 1 year-old; 2 years-old; 8-years-old sites, respectively) showed significantly lower numbers of seeds (paired *t*-test, *p* value < 0.001) than the control transects (2533 ± 1701; 2578 ± 1114; 3578 ± 4585 seeds*m^{-2} for 1 year-old; 2 years-old; 8-years-old sites, respectively).

The number of seeds found at the different accumulation zones at the burned transects is shown in Fig. 6. Thereby, a clear trend of lower seed availability was observed for all fire events at zone 1.

The OLS linear regression model describing the seed availability at the burned transects is shown in Table 4. This model outperformed models based on a Poisson distribution, which violated the assumption of constant variance (overdispersion) (Wood 2017). The same variables as for the analysis of the accumulated soil material (Table 2) were tested, and soil accumulation was included. Accordingly, the number of seeds is significantly influenced by the accumulation zone ($p < 0.01$) and age of fire event ($p = 0.012$) as well as mean annual precipitation ($p = 0.017$). The variables used to describe the number of seeds in the deposited soil material explained 33.5% (adjusted R^2) of the variance.

Soil accumulation and seed availability

The "Pearson" correlation coefficient between the number of seeds and accumulated soil material is 0.27. Figure 7 shows the results of a fitted logarithmic curve to describe the correlation between available seeds and the accumulated soil material.

Discussion

Soil accumulation and seed availability

The two variables that had a significant influence on soil redistribution and the number of seeds were the time (years) since the fire event and the position in the slope zones. The number of years since the fire event had the greatest influence on the total accumulated soil material and seeds (Fig. 4, Table 2). However, annual soil accumulation rates decreased as time passed after the fire event. This finding is supported by other studies,

Table 3 Mean number of intact seeds [count*m^{-2}] of the identified species and unidentified seeds (rounded). Horizontal solid double line separates study sites, horizontal dashed line separates mean values per study site from mean values of the study locations, horizontal solid line separates burned (grey shaded) from control from transects (see Table 1, Fig. 2), and vertical dashed line separates tree, shrub, herb, not identified seeds and fruits

Study Site with age (year), status (burned-control), and forest type	*N. antarctica*	*N. dombeyi*	*A. chilensis*	*M. boaria*	*P. ponderosa*	*Schinus patagonica*	*Ovidia andina*	*Aristotelia chilensis*	*Beberis* spp.	*Discaria chacaye*	*Diostea juncea*	*Alstroemeria aurea*	*Vicia nigricans*	not identifiable	*Muehlenbeckia hastulata* fruits
Steffen mean burned 1 year (2022)	-	-	58	6	-	-	-	487	-	-	87	-	4	9	2
Mb – burned *A. chilensis* with *N. dombeyi*	-	-	89	4	-	-	-	363	-	-	22	-	7	4	-
Sb – burned *A. chilensis* with *N. dombeyi*	-	-	26	7	-	-	-	611	-	-	152	-	-	15	4
Steffen mean control 1 year (2022)	-	45	1,067	675	-	72	-	956	11	-	311	-	-	-	-
Mc – control *A. chilensis* with *N. dombeyi*	-	78	2,122	89	-	144	-	833	-	-	44	-	-	-	-
Sc – control *A. chilensis* with *N. dombeyi*	-	11	11	44	-	-	-	1,078	22	-	577	-	-	-	-
Piltriquitrón mountain range mean burned 2 years (2021)	-	67	185	-	-	6	-	254	-	-	-	-	2	45	-
Gb – burned *A. chilensis* with *N. dombeyi*	-	4	56	-	-	7	-	218	-	-	-	-	-	67	-

Table 3 (continued)

Study Site with age (year), status (burned-control), and forest type	*N. antarctica*	*N. dombeyi*	*A. chilensis*	*M. boaria*	*P. ponderosa*	*Schinus patagonica*	*Ovidia andina*	*Aristotelia chilensis*	*Beberis* spp.	*Discaria chacaye*	*Diostea juncea*	*Alstroemeria aurea*	*Vicia nigricans*	not identifiable	*Muehlenbeckia hastulata* fruits
Rb – burned *A. chilensis* with *N. dombeyi*	-	130	315	-	-	4	-	289	-	-	-	-	4	22	-
Piltriquitrón mountain range mean control 2 years (2021)	-	50	1,728	11	-	33	17	717	-	22	-	-	-	-	-
Gc - control *A. chilensis* with *N. dombeyi*	-	67	1,411	-	-	44	-	1,411	-	-	-	-	-	-	-
Rc – control *A. chilensis* with *N. dombeyi*	-	33	2,044	22	-	22	33	22	-	44	-	-	-	-	-
Cholila mean burned 8 years (2015)	24	-	170	56	-	41	134	542	2	65	34	8	11	65	1,809
Cb – burned *A. chilensis* with *N. antarctica*	48	-	15	63	-	44	263	570	4	-	67	15	11	11	3,574
Hb – burned *A. chilensis*	-	-	326	48	-	37	4	514	-	130	-	-	11	118	44
Cholila mean control 8 years (2015)	6	-	878	44	6	72	89	1,400	-	67	83	-	-	50	6
Cc – control *A. chilensis* with *N. antarctica*	11	-	33	67	11	133	-	78	-	133	166	-	-	100	11
Hc – control *A. chilensis*	-	-	1,722	22	-	11	178	2,722	-	-	-	-	-	-	-

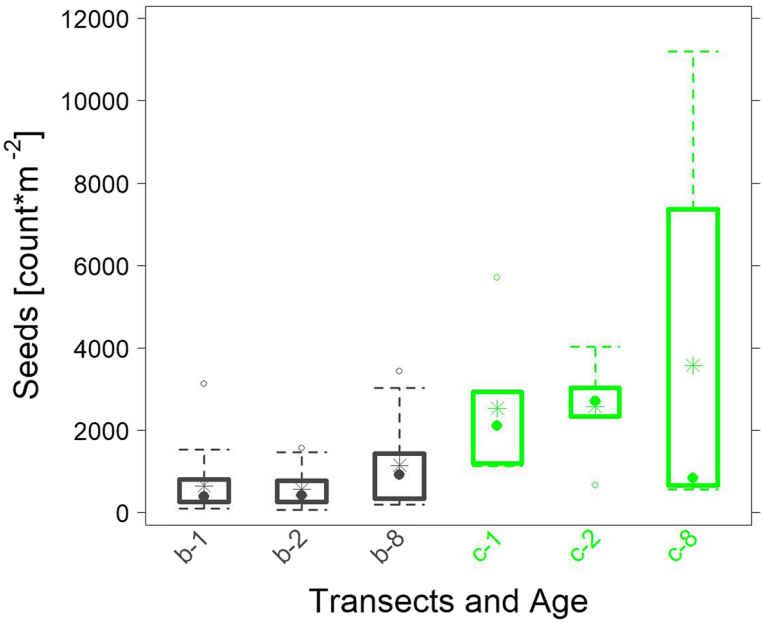


Fig. 5 Number of intact seeds found on the burned and control transects. b: burned, b-1 (2022), b-2 (2021), b-8 (2015) (n = 3*18) in gray; c: control, c-1 (2022), c-2 (2021), c-8 (2015) (n = 3*6) in green; points: median values; asterisk: mean values; whiskers = 1.5*interquartile range

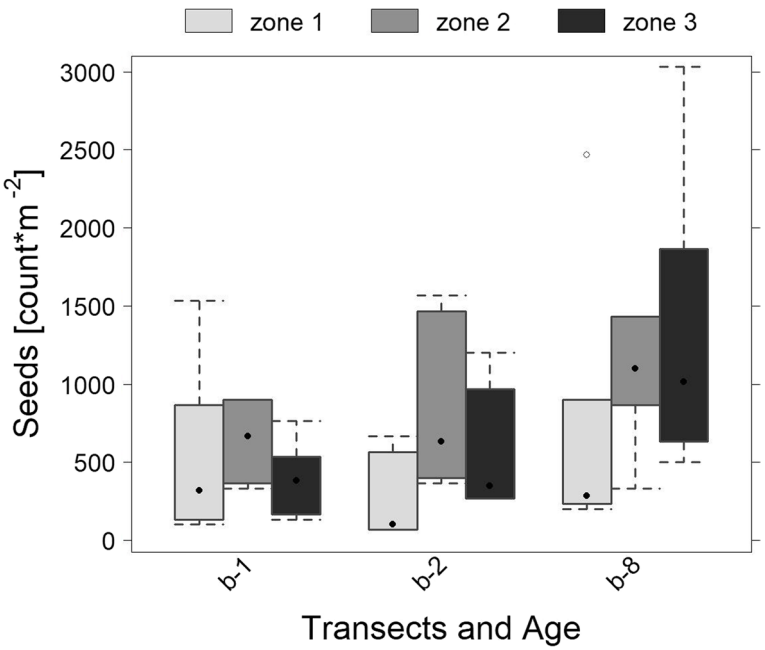


Fig. 6 Number of intact seeds in the burned transects at different accumulation zones. Fire events b-1 (2022), b-2 (2021), b-8 (2015); points: median values; whiskers = 1.5*interquartile range

which indicate that the risks of erosion are the highest in the first year following wildfire (Robichaud et al. 2000; Fernández and Vega 2016). Nevertheless, erosion was still observed up to 3 years after forest fires by Kim et al. (2008) and, according to a review by Shakesby and Doerr (2006), a decline in background erosion rates after 5 to 8 years. The slope position, described by the different accumulation zones, is the second variable that explains the amount of accumulated soil material. At recent fire events, soil accumulation was the highest

Table 4 Results of the OLS linear regression for the logarithmic transformed seed availability at the burned transects as response variable

Predictor variables	Estimate	Standard error	Significance
Intercept	−6.716	3.784	0.083
Age: 2 (2021); compared to age 1 (2022)	2.106	0.952	0.032
Age: 8 (2015); compared to age 1 (2022)	1.981	0.608	0.002
Accumulation zone: 2; compared to zone 3	0.402	0.266	0.137
Accumulation zone: 1; compared to zone 3	−0.646	0.266	0.018
Mean annual precipitation	0.005	0.002	0.017

Model results: *F*-statistic (df = 48) 6.388, $p < 0.0002$; multiple $R^2 = 0.398$, adj. $R^2 = 0.335$. Model: lm(log(seed availability) ~ factor(age) + accumulation zones + mean annual precipitation); tested but not significant or highly intercorrelated variables are slope inclination [°]; slope aspect; study site; forest type, accumulated soil material (Fig. 4)

at slope zone 3 and the lowest at zone 1. As time progressed since the fire event, the differences between the three sampled accumulation zones disappeared. However, it is important to note that the length of the slopes varied between the sampling locations, so that zone 3 was not always located at the area of maximum accumulation. In addition, the applied sampling methodology, to only a depth of 10 cm, could underestimate thick soil accumulations at older forest fire events. This is particularly true for the 8 years-old study locations (Table 1, Fig. 2), and the reported values must be considered as the minimum accumulated soil material. This also explains why no differences could be detected between the individual accumulation zones at this study location (Fig. 4). However, our estimated soil accumulation is within a realistic range, as individual rainfall simulations after forest fires showed sediment production of 0.2 to 1.0 $kg^{*}m^{-2}$ with a background erosion rate of 0.004 $kg^{*}m^{-2}$ for *A. chilensis* forests in Patagonia (Morales et al. 2013). In contrast, unburned shrubland transitioning to steppe showed lower erosion rates (0.02 to 0.06 $kg^{*}m^{-2}$), attributed to desert pavement (César 1989). Another variable that showed statistical significance in the soil accumulation was the slope aspect (Table 2), particularly the southwest aspect, which is directly related to the Southern Hemisphere westerlies—prevailing winds from the west towards the east (Chen et al. 2015). This exposes southwest-facing slopes to wind and rain events and is expected to result in greater erosion after forest fires.

In general, it is difficult to disentangle the redistribution of seeds with soil material from other effects of seed input, such as seed dispersal by gravity, wind, animals, or water (Howe and Smallwood 1982). Consequently, the results obtained are restricted to the general concept of seed availability. In our study, fire events from recent years had accumulated soil material of around 2 and 4 cm thickness after 1 and 2 years, respectively. According to Wolters and Bakker (2002), most of the seeds from established vegetation redistributed by precipitation are located in the upper soil layer from 0 to 5 cm. The sites with a fire event 8 years ago had a higher soil accumulation, reaching up to 15 cm thickness, but even at those locations, the number of seeds remained constant after a certain amount of accumulated soil (Fig. 7). Also seed dispersal shows a high spatio-temporal variability (Herrera et al. 1998; Nathan and Muller-Landau 2000), which is also reflected in our data (Table 3). In addition, the lower number of samples in the control ($n = 18$) transects may explain some of the high variability in the control transects compared to the burned transects ($n = 54$) (Fig. 5). In addition, potential edge effects within the transect distances (Fig. 3) from the intact stand edge cannot be completely excluded (Melo et al. 2006; Baker et al. 2013). These effects may be positive or negative and can be influenced by factors such as the abundance of granivores and dispersers (Vazquez et al. 2022), flowering, seed production (Pollock et al. 2017), and microclimatic wind turbulence. Nevertheless, the transects at the burned forest sites show significantly lower numbers of seeds than the control transects. Our study confirms that seed availability and soil accumulation change along the slopes, and the latter may ultimately also affect soil productivity, as shown by Khan et al. (2013).

Impact and changes in site conditions

The influence of topography on soil redistribution and seed availability is also notable in this study through the different accumulation zones. However, slope inclination was not found to have a significant impact on accumulated soil material (Table 2) and the number of seeds (Table 4). This may be attributed to the study site selection with a homogenous slope inclination of 24 to 33° (Table 1). In other studies (Wang et al. 2023), slope inclination showed a significant positive correlation with eroded sediment in uniform slopes. We did not record

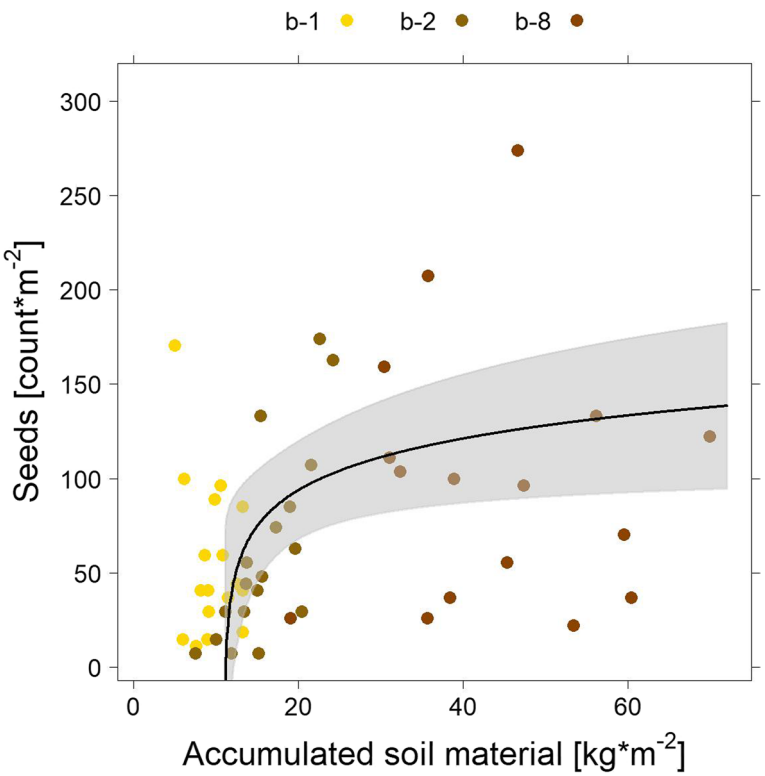


Fig. 7 Correlation between the number of seeds and accumulated soil material at the burned transects differentiated by the time since of the fire events. b-1 (2022), b-2 (2021), b-8 (2015); gray shaded area indicate 95% confidence intervals. Model: seed availability ~ log(accumulated soil material−11). Model results: *F*-statistic (df = 37) 6.88, $p < 0.01258$; multiple $R^2 = 0.16$, adj. $R^2 = 0.13$

other variables, such as surface roughness, which can provide insights into the micro-topography of the slopes (Grundy et al. 2020) and further describe the observed accumulation patterns. It has been shown that vertically convex slopes have more sediment production than concave slopes (Rieke-Zapp and Nearing 2005). In addition to slope-related factors, other site characteristics, such as vegetation cover, soil properties, or post-fire downed logs or standing deadwood (snags), play an important role in the processes of infiltration, revegetation, and forest restoration (Urretavizcaya and Defosse 2019), thus directly influencing the acceleration of soil material redistribution by runoff.

The ecosystem response to fire in terms of carbon storage and nutrient cycles of Patagonian Andosols is expected to be less significant compared to crystalline soils, mainly due to their generally high organic matter content and lower mineralization rates (Alauzis et al. 2004; La Manna and Barroetaveña, 2011). Additionally, the high porosity (low bulk density) of the Andosols (Buduba et al. 2020) has an insulating effect on thermal conductivity (Abu-Hamdeh and Reeder 2000), which is likely to reduce negative effects on deeper soil horizons. However, the study by Alauzis et al. (2004) suggests that post-fire productivity and regeneration of subalpine *Nothofagus pumilio* ((Poepp. & Endl.) Krasser) forests in northwestern Patagonia are strongly related to changes in soil properties, particularly those affecting nitrogen and water dynamics. These changes in soil properties could therefore be critical in influencing the overall vegetation recovery and growth after fire. However, a study by Kitzberger et al. (2005) suggests that these negative effects disappear over time and that vegetation recovery and growth may be more related to fire severity and limited seed bank than to soil fertility (Varela et al. 2006).

Species traits and vegetation recovery

In our study, we focused on analyzing the presence of seeds from woody species (>1.4 mm) after forest fire events and not on seed viability. Most of the collected seeds, especially from the burned transects, exhibited a blackened appearance. Consequently, most seeds found in our burned areas could be determined as non-viable. This could be due to the sampling time at the end of spring. Seed dispersal occurs in the autumn and many seeds begin to germinate in the spring, following winter stratification. Furthermore, seed quality varies among species and decreases with time (Urretavizcaya et al.

2016). Studies by Raffaele and Gobbi (1996) and Urretavizcaya and Defosse (2004) found that the proportion of viable seeds of *A. chilensis* decreases sharply as the season progresses, from the seed rain in May to the late summer of the following year (February). However, fire events have negative effects on seed viability, induce seed death through complete burning, overheating, and desiccation (Bradstock and Auld 1995; Auld and Denham 2006), and germination rates due to depletion of soil nutrients and water storage capacity (Jiao et al. 2009). Thus, the continuous input of seeds from intact forest patches and from post-fire vegetation is important in contributing to the recruitment of new individuals from seeds. Accordingly, the same number of woody species (9) was found in the burned and unburned forest at the 8 years-old sites, and a lower number was found in the burned (4) than in the unburned (7) forests at the 1 year and 2 years-old sites (Table 3). This suggests that as the vegetation recovers, seed diversity increases, promoting vegetation recovery and successional processes. Following high-severity fires that affect large areas, the lack of surviving seed trees becomes a critical factor for natural tree regeneration. Despite the proximity to the intact forest edge and thereby potential seed sources, the burned transects revealed a significantly lower number of seeds compared to the control transects. In addition, the analysis of the seed availability indicates that the overall seed production is positively influenced by the mean annual precipitation at the sites. The controlling effect of precipitation on seed production, at least during resource priming (1 to 2 years before seed production), is in line with findings by Keeley (1977) in post-fire chaparral in California, USA, or Smaill et al. (2011) for a *Nothofagus* species in New Zealand.

We found *A. chilensis* to be the most common species among tree seeds, as it is widespread in different forest sites, including wind-exposed slopes, valley bottoms, poorly drained wetlands (*mallines*), and arid and wind-exposed sites (Veblen et al. 2003; La Manna and Barroetaveña, 2011). Among shrub species, *Aristotelia chilensis* seeds were the most abundant in all sites and locations, suggesting that regeneration from seeds of this species is very important in the first stage of post-fire succession in the region. The observation of seedlings of this species a year after the "Golondrinas" fire, in Piltriquitrón mountain range, by Rago et al. (2024) supports this finding. In addition, *N. antarctica*, *N. dombeyi*, and *D. juncea* were the most abundant woody species in the germinable soil seed bank surveyed in autumn, immediately after the "Las Horquetas" fire, in Cholila by Williams et al. (2018). In that study, the high abundance of *Nothofagus* spp. was explained by the seed rain that occurred after the fire. In addition, the examination of germinable soil seed banks in other burned forests in the region revealed a potential contribution of woody species seeds to post-fire revegetation (Raffaele and Gobbi 1996; Urretavizcaya et al. 2022).

At the recently burned Lago Steffen (2022) sampling site, we observed an initial vegetation stage dominated by the bryophyte *Funaria hygrometrica* (Hedw.). This observation is consistent with the findings of Duncan and Dalton (1982), who reported that this particular bryophyte showed a preference for germination on burnt soils. Esposito et al. (1999) also reported that *F. hygrometrica* is one of the most dominant bryophyte species following severe fire events in Mediterranean vegetation, showing rapid development of both gametophytes and sporophytes. In general, rapid recolonization by biocrust-forming mosses in the first years after forest fire plays an important role in succession and reduces topsoil erosion, nutrient loss (Ryömä and Laaka-Lindberg 2005; Morales et al. 2013), and controls water erosion (Silva et al. 2019; Gall et al. 2022; García-Carmona et al. 2023).

It is evident that many native species have the capability to quickly colonize sites after fire, and the regeneration of species can occur far from seed sources, thanks to pre-fire and post-fire distribution patterns of seeds (Kiel and Turner 2022). The presence of a persistent seed bank and a short period of favorable conditions immediately after wildfires are critical to the maintenance of viable populations for many early succession specialist plants. Seed banks may renovate during this short window of recruitment after lying dormant for years between wildfire cycles (Lee 2004). This may be the case of *Muehlenbeckia hastulata*, a climbing shrub that germinates early after fire covering the soil surface and after a few years it decreases its cover or even disappears (Gobbi et al. 1995), and which seeds and fruits remain in the soil for many years, as it was detected in the older fire site (Table 3). Understanding these traits, associated with resistance and recovery from fire, is crucial for predicting the future development of the vegetation following fire disturbances.

Opportunity for non-native species

In addition to soil redistribution and seed availability, the occurrence of fires raises another important issue which is the high risk of spreading of non-native and invasive species (Turner et al. 1999; Fernández and Vega 2016). In Patagonia, a great number of non-native plant species have been introduced since the beginning of the last century as a result of European immigration (Rovere et al. 2013), particularly tree species for forestry purposes (Simberloff et al. 2002; Iglesias et al. 2022). This poses problems for nature conservation, forestry, and fire management. For example, poor or no forest management

in conifer plantations (e.g., no thinning or fire breaks) can further increase the potential for crown fire spread. Some of these species are also well-adapted or even favored by fire. Despite the fact that our study locations are surrounded by native forests, we still encountered a *P. ponderosa* seed at the Cholila (2021) site. This area is located approximately 250 m from a plantation of the exotic conifer *P. ponderosa* (CIEFAP and MAyDS, 2016). Although not close to our sampling sites, this indicates the possibility of long-distance dispersal capability of its seeds. Therefore, forest fires can be a window of opportunity for the spread of non-native species as well (Raffaele and Gobbi 1996; Franzese and Raffaele 2017; Rago et al. 2024).

Conclusion

Following high-severity fire events, general patterns of soil redistribution and seed availability can be observed. As time since the fire event increases, the amount of redistributed soil material and the number of seeds increases. However, the pattern of soil accumulation and consequently the number of seeds varies across the slope. In the backslope position, seed availability is low compared to the toeslope although the amount of accumulated soil material converges over time. In addition, southwest-facing slopes have significantly higher soil accumulation than south-facing slopes. With this understanding, it is reasonable to infer that regeneration will start initially at the bottom of the slopes and gradually move uphill, with the more degraded soils at the upper slope positions being the last to be revegetated.

Among the recorded species, the tree *A. chilensis* and the shrub *Aristotelia chilensis* emerge as key players in post-fire recovery, with the highest number of seeds at all study locations. However, the number of seeds was always greater in the unburned than in the burned forests. Besides, the number of shrub seeds was greater than that of tree seeds both in the burned and unburned forests. This may lead to the shrub predominance, at least, in the early post-fire succession.

Forest restoration after disturbance, whether passive through natural processes or through forest management, e.g., seeding or planting trees, is therefore a global challenge (Zerbe 2023). Understanding the risk of soil redistribution and seed availability will assist restoration efforts and ecosystem management.

Acknowledgements
The authors would like to thank Marcelo Bari and Anabella Carp of the National Park Authority (APN), Danilo Ramirez of the Andean Forest Service (SFA), and Stefano Gianolini and Virginia Alonso of CIEFAP for their help with sampling, as well as the landowners where the study was carried out and Thomas Sansone for support with graphics.

Authors' contributions
Conceptualization: A.S., S.Z., C.G.; methodology: A.S., S.Z., C.G., M.M.R., M.F.U.; investigation: P.B.A., M.M.R., M.F.U.; formal analysis and visualization: A.S., P.B.A., M.F.U.; project administration and funding acquisition: H.W., C.G., S.Z.; writing—original draft: A.S., P.B.A., S.Z.; writing—review and editing: all authors.

Funding
Open Access funding enabled and organized by Projekt DEAL. The study is imbedded in the international and interdisciplinary research project "Sustainable forest management of temperate deciduous forests – Northern hemisphere beech and southern hemisphere beech forests" (KLIMNEM), which is supported by funds of the Federal Ministry of Food and Agriculture (BMEL), based on a decision of the Parliament of the Federal Republic of Germany via the Federal Office for Agriculture and Food (BLE, grant No. 503 28I-042–01). The international mobility program of the University of Innsbruck provided financial travel funds for the field-work in Argentinean Patagonia.

Data availability
The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author details
[1]Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Göttingen, Germany. [2]Institute of Geography, University of Innsbruck, Innsbruck, Austria. [3]Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, Bozen, Italy. [4]Andean Patagonian Forest Research and Extension Center (CIEFAP), Esquel, Argentina. [5]National Council for Scientific and Technical Research (CONICET), Esquel, Argentina. [6]Institute of Geography, University of Hildesheim, Hildesheim, Germany.

Received: 19 April 2024 Accepted: 6 February 2025
Published online: 11 March 2025

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