

Article

Early Vegetation Recovery After the 2008–2009 Explosive Eruption of the Chaitén Volcano, Chile

Ricardo Moreno-Gonzalez^{1,2,*} , Iván A. Díaz¹, Duncan A. Christie^{1,3,4}  and Antonio Lara^{1,3}

¹ Instituto de Conservación, Biodiversidad y Territorio, Universidad Austral de Chile, Valdivia 5090000, Chile; ivan.diaz@docentes.uach.cl (I.A.D.); duncanchristieb@gmail.com (D.A.C.); antoniolar@uach.cl (A.L.)

² Calahuala Cooperative, Valdivia 5090000, Chile

³ Center for Climate and Resilience Research (CR)2, Valdivia 5090000, Chile

⁴ Cape Horn International Center for Global Change Studies and Biocultural Conservation (CHIC), O'Higgins 310, Puerto Williams 6350000, Chile

* Correspondence: ricardo.moreno@uach.cl

Abstract: In May 2008, Chaitén volcano entered an eruptive process, leading to one of the world's largest eruptions in recent decades. The magnitude of tephra ejected by the eruption left different types of disturbances and caused diverse forms of environmental damage that were heterogeneously distributed across the surrounding area. We went to the field to assess the early vegetation responses a year after the eruption in September 2009. We evaluated the lateral-blast disturbance zone. We distributed a set of plots in three disturbed sites and one in an undisturbed site. In each of these sites, in a rectangular plot of 1000 m², we marked all standing trees, recording whether they were alive, resprouting, or dead. Additionally, in each site of 80 small plots (~4 m²), we tallied the regenerated plants, their coverage, and the log volume. We described whether the plant regeneration was occurring on a mineral or organic substrate (i.e., ash or leaf litter, respectively). In the blast zone, the eruption created a gradient of disturbance. Close to the crater, we found high levels of devastation marked by no surviving species, scarcely standing-dead trees and logs, and no tree regeneration. At the other extreme end of the disturbance zone, the trees with damaged crowns were resprouting, small plants were regrowing, and seedlings were more dispersed. The main form of regeneration was the resprouting of trunks or buried roots; additionally, a few seedlings were observed in the small plots and elsewhere in disturbed areas. The results suggest that the early stages of succession are shaped by life history traits like dispersion syndrome and regeneration strategy (i.e., vegetative), as was found after other volcanic eruptions. Likewise, the distribution of biological legacies, which is related to disturbance intensity, can cause certain species traits to thrive. For instance, in the blow-down zone, surviving species were chiefly those dispersed by the wind, while in the standing-dead zone, survivors were those dispersed by frugivorous birds. Additionally, we suggest that disturbance intensity variations are related to the elevation gradient. The varying intensities of disturbance further contribute to these ecological dynamics. The early succession in the blast zone of Chaitén volcano is influenced by the interaction between species-specific life history, altitudinal gradient, and biological legacies. Further studies are required to observe the current successional patterns that occur directly in the blast zone and compare these results with those obtained following other volcanic disturbances.



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1. Introduction

Volcanic eruptions are large-scale disturbances that modify the composition, structure, and ecosystem processes [1–3]. As volcanoes enter the eruptive phase, a complex mechanism of events is involved in multiple types of disturbances, such as explosive blasts, block and ash flows, thermal and toxic chemical waves, landslides, glowing avalanche deposits, debris flows, lava flows, and the air fall of volcanic tephra [1,4]. As a consequence, eruptions can have effects at very large spatial and temporal scales [5,6], as well as direct effects on the surrounding forest through burning, burying, and/or blowing down trees or other plants [4]. However, since this kind of large disturbance is infrequent [2] and has seldom been monitored [7], our understanding of vegetation responses remains limited. The effect of volcanism has been studied by comparing different stands in chronosequences, assuming that different forest patches reflect different successional stages after the disturbance, e.g., [8–11]. Despite the importance of volcanic eruptions, few studies have analyzed the effect of eruptions shortly after the event [4,7]. Notwithstanding this, important contributions have been made to research on plant community dynamics. These include studies conducted after the 1996 eruption of Mount Koma in northern Japan [12], the 1907 Ksudach volcano eruption in the Kamchatka Peninsula [13], the eruption of Mount Oyama in Miyake-Jima Island, Japan [14], and many others in the Northern Hemisphere. While in the Southern Hemisphere, related studies are largely concentrated in New Zealand [15,16].

Forest recovery is considerably slow following disturbances that heavily impact the soils as well as the aboveground vegetation [17]. Although volcanoes are considered catastrophic disturbance events, it is possible for diverse biological legacies to remain after the event. As observed after the eruptions of Mount St Helens, the persistence and heterogeneous distribution of these biological legacies can aid the recolonization of plants [2,18]. For example, the life history traits of the pre-disturbed community could mean that particular survivors are perhaps able to recolonize and expand under the new conditions presented by the disturbed environment [2,18]. Therefore, the arrangement and amount of such biological legacies could influence the rate and pathways of new colonizers. The recovery rate is negatively related to the distance from the undisturbed area [19].

One of the most active tectonic and volcanic areas in the world corresponds to the subduction area of the Nazca and the South American plate, e.g., [20], which also contains the longest and the second-highest mountain range in the world, the Andes. The volcanoes in the Chilean Andes are quite active. The Southern and Austral Volcanic Zones comprise 74 volcanoes that have been active since the post-glacial period (~17 ka) up to the present, and at least 21 have had one large explosive eruption (Volcanic Eruptive Index ≥ 5) [21]. The South American temperate rainforest (SATR) is located in the south of the Andes [22]. This cordillera plays a critical role in the SATR dynamics, where the current successional models after volcanic disturbances suggest that the *Nothofagus* are dominant pioneer trees that benefit from such disturbances [23]. The SATR represents a biogeographical island that is rich in endemic species and dominated by evergreen, broad-leaved species [24–26]. South of 40° S, extensive areas of old-growth forest dominate the mountainous landscape. These forests are not directly disturbed by modern human activities and represent one of the last pristine areas with pre-industrial biogeochemical conditions [27].

In May 2008, the last eruption of the Chaitén Volcano (42°50' S) started near the small town of Chaitén in southern Chile (Figure 1, left panel). This eruption was the largest rhyolite eruption since the great eruption of Katmai Volcano in 1912 and the first rhyolite eruption for which some attributes of its dynamics and impacts were monitored [28]. The eruption consisted of an approximately 2-week-long explosive phase that generated as much as 1 km³ bulk volume tephra (~0.3 km³ dense rock equivalent), followed by an approximately 20-month-long effusive phase during which 0.8 km³ of high-silica rhyolite

lava erupted, forming a new dome within the volcano's caldera [28]. Chaitén Volcano was surrounded by extensive old-growth forests undisturbed by humans, providing a unique opportunity to evaluate the effects of volcanism over an undisturbed landscape.

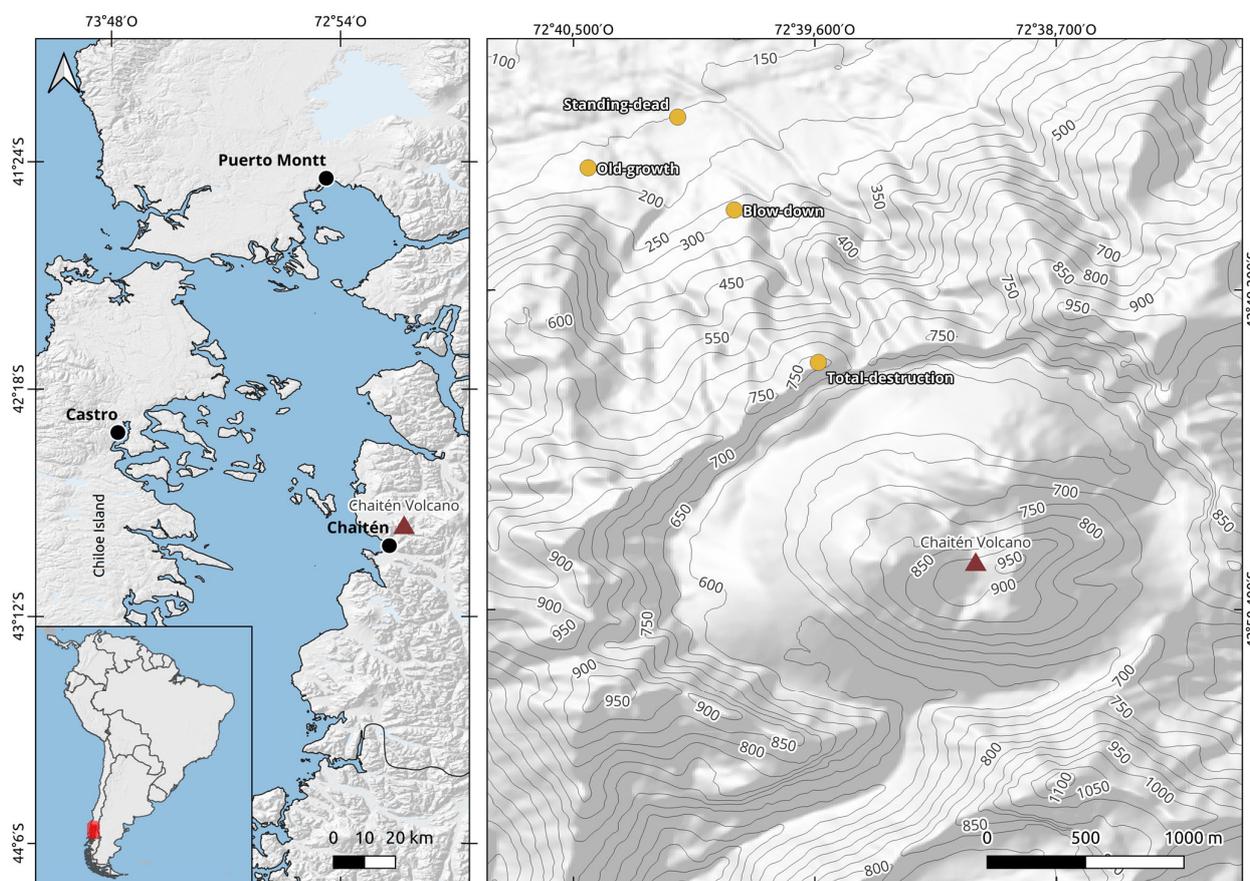


Figure 1. Map of the study site. (Left panel) indicates the position of Chaitén Volcano (red triangle) in relation to the main cities (black dots). (Right panel) shows a close-up of the volcano's blast zone, the plots' distribution along the disturbance/elevation gradient (total-destruction plot, blow-down plot, and standing-dead plot), and the undisturbed sector (old-growth plot).

In this study, we characterized the early establishment of vegetation after the eruption of Chaitén Volcano along a disturbance gradient one year after the eruption started, from near the crater to the closest old-growth forest with vegetation completely alive. We predict that plant species diversity and the number of living trees will decrease close to the crater, and pioneering *Nothofagus* species are colonizing the areas affected by the eruption. Our objectives included the creation of a baseline for further long-term monitoring of the vegetation that is recovering and to identify and analyze the importance of biological legacies for forest recovery.

2. Material and Methods

2.1. Study Site

Chaitén Volcano is located on the west side of the Andean Range in southern Chile, at 42°50' S and 72°39' W (Figure 1), and is part of the so-called Southern Volcanic Zones. Chaitén Volcano is a dome of ~1100 m above sea level, located 10 km NW of the town of Chaitén, populated by approximately 5000 inhabitants before the eruption (Figure 1). The climate of the area corresponds to a humid temperate with a strong oceanic influence [29]. The landscape is characterized by sharp mountains shaped by glaciers and valleys originating from fluvial and glacio-fluvial outwash [1]. Vegetation within the influence area

of Chaiten Volcano is dominated by a dense old-growth temperate rainforest of northern Patagonian and Valdivian types [1,29–31]. These forests' compositions are dominated by broad-leaved evergreen trees such as *Nothofagus dombeyi* (Mirb.) Oerst. (Nothofagaceae), *Laureliopsis philippiana* (Looser) Schodde, *Gevuina avellana* (Molina), *Amomyrtus luma* (Molina) D. Legrand and Kausel, *Luma apiculata* (DC.) Burret, *Drymis winteri* J.R. Forst. and G. Forst., *Eucryphia cordifolia* Cav., and *Weinmannia trichosperma* Cav. (both Cunoniaceae). These species are normally arranged in multi-layered canopy strata and old, large emergent trees (up to c. 40 m height) and abundant snags and logs. The understory is densely covered by ferns, such as *Lophosoria quadripinnata* (J.F.Gmel.) C.Chr. and *Blechnum magellanicum* (Desv.) Mett., seedlings, saplings, and bamboo tickets (*Chusquea* spp.). Specific plant composition and structure previous to the disturbance are not available because it was an area largely unexplored.

2.2. Study Design

We carried out the fieldwork in September 2009. We first conducted a general inspection of the study area as suggested by del Moral [32]. Later, we selected four sites with different degrees of volcanic impact (Figure 1), following similar classifications of previous studies [32]. The first site corresponds to a forest with low volcanic impact that only received a few millimeters of tephra deposition. This site is called “Old-growth forest”. It is located 5 km from the center of the new dome at an elevation of 600 m a.s.l. (Figure 1, right panel). The second site is characterized by the presence of abundant dead-standing trees and higher tephra deposition. This site is called the “Standing-dead” plot and is located 3.5 km from the center of the new dome at 160 m a.s.l. The third site was more affected by the eruption and is characterized by high tephra deposition, where most trees are broken or blown over by the eruption. This site is called “Blow down” and is located 2.3 km from the center of the new dome at an elevation of 300 m a.s.l. Finally, the fourth and most affected site is on the border of the crater at 1.5 km from the center of the new dome and at 750 m a.s.l. This site presented the higher tephra deposition, and all trees were blown down by the eruption and heavily buried under volcanic ash. This site is called “Total destruction”.

In each one of these four areas was installed a 50 × 20 m permanent plot, where we measured the diameter at the breast height (dbh) of all trees ≥ 5 cm in diameter. Every tree was identified at the species level when possible and labeled with a numbered aluminum tag. We registered if the stems were alive, resprouting after the eruption, or snags (standing-dead stems). To estimate the presence and abundance of tree regeneration, we traced four transects 120 m long. The transects were distributed parallel, separated 20 m from each other. In each transect, we mounted five circular plots of 1.5 m radius (4.71 m²) every 30 m. On these plots, we counted all seedlings and saplings present and recorded the substrate where they were rooted (forest soil, logs, or volcanic tephra). We registered other non-tree plant species in the circular plots, estimating their abundance as the relative cover, and also recorded if the substrate where they were rooted was organic or mineral (e.g., forest soil, logs, or volcanic tephra). We assessed the volume of all exposed logs within the plots. Assuming a cylindrical form of each log, we calculated the volume of logs present inside the plot and standardized its measurements to m³ of logs per m² of plot surface.

2.3. Data Analysis

The species richness of tree seedlings, herbs, and shrubs was compared among sites using rarefaction analysis. Rarefaction curves allow for comparing species richness among environments, avoiding the bias in the number of species detected due to the increased probability of species detection in areas where individuals were more abundant, by plotting

the number of species detected in the function of the number of individuals observed [33,34]. This procedure includes Monte Carlo simulations delivering an average value of species richness with a confidence level of 95% (Colwell 2006) [35]. Rarefaction analyses were conducted using the free software EstimateS Win 8 [35]). Non-vascular species were excluded from the rarefaction analyses since not all of them were classified up to the species level, and one genus could include several species. Plant composition among sites was compared using Sørensen's similarity index based on the presence/absence of plant species. Rarefaction and similitude analyses were both carried out with the software EstimateS Win 8 as well. In attempting to define if the plant composition of one site was a subset of the composition of another site, we conducted a nested analysis in NestCalc v.1 [36,37].

3. Results

3.1. General Description of the Effects of the Eruption

The eruption of Chaitén Volcano has an impressive effect on the forest and landscape (Figure 2). The eruption in the study area produced a gradient of destruction (Figure 2B,C). Around the crater, all the trees were blown down and heavily buried by tephra. Other trees were partially buried and/or broken in half, with the trunks covered with the impact marks of many little stones—this resembled damage caused by gunfire (Figure 2A,D). Moving away and down from the crater, trees were blown down and densely covered by ash (Figure 2E), while further away, trees were standing deadwood ('snag'), presenting progressively finer branches (Figure 2F). Many small patches of organic litter were exposed and sparsely distributed and protected from the direct effect of the eruption by root discs and large trunks or were exposed by small ravines that flush away the volcanic ash. These small patches looked like clumps of organic soil, with roots of ferns and other small plants that were not buried by the tephra. These clumps were covered by plants that survived in the area affected by the eruption, and their frequency increased when moving away from the crater toward the undisturbed forests (Figure 2G).

In the surrounding area, we did not observe evidence of fire caused by the eruption, but the trunk and bark of several trees looked charred within the influence area. Trees were dead and dry from the eruptive explosions, but some trees in the blow-down and standing-dead areas maintained bark on the opposite side of the crater, perhaps with possibilities to resprout hereafter. Tephra buried the fallen trees in the whole study area, but principally in the blow-down and total-destruction areas. Here, the tephra was very compacted, seeming like pavement that covered the fallen forests. Heterogeneous tephra deposition exposed some trunks, clumps, and remnants with organic forest soil that was likely from the original forest. Shrubs and epiphytes were spread everywhere in the standing-dead area. Ferns, bamboo, and tree seedlings were growing in remnants of exposed organic soil, usually below or at one side of trunks or unearthed roots. Surviving trees increased when moving away and down from the crater.

3.2. Species Composition

We found 10 species of trees in the area and 50 species of smaller plants, including seedlings, herbs, and ferns (Table 1). The rarefaction analysis for tree species showed that the standing-dead plot held one more species than the old-growth forest plot (Figure 3). This same analysis showed that the blow-down plot held very few individuals, but the initial slope and shape of the curve were similar to the other two curves, indicating that all curves showed a similar number of tree species. The rarefaction analysis of small vascular plants showed that the old-growth forest site had the richest species composition while decreasing in the standing-dead and blow-down plots (Figure 3). The total-destruction plot showed practically no species.

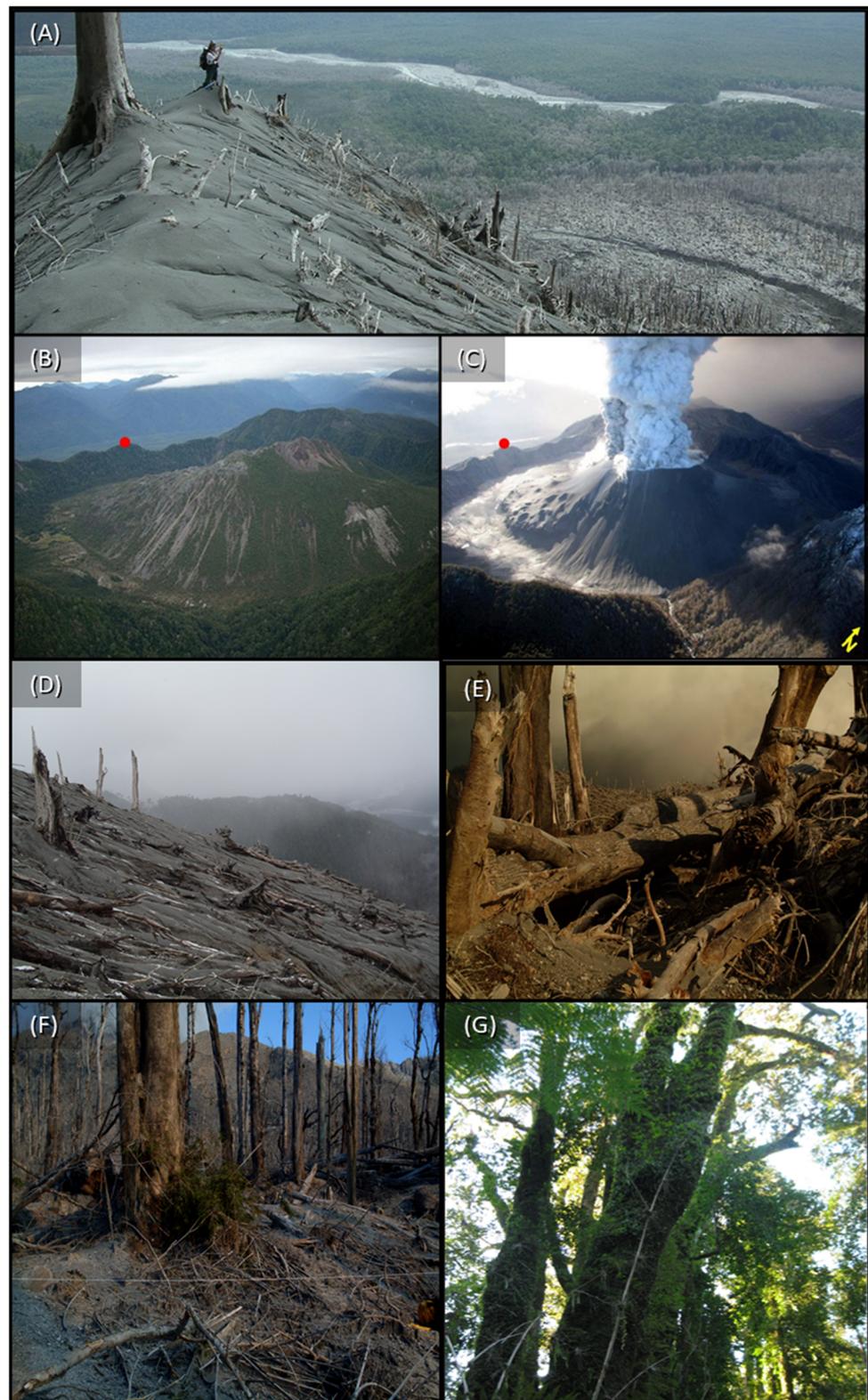


Figure 2. Photographic records of the study site. (A) showing impressive impacts close to the crater. Comparison of the volcanic dome and vegetation cover before (B) and during the 2008–2009 eruption (C). Red dot indicates the approximate position of the researcher (Dr. Díaz) in panel (A). Images (D–G) represent a disturbance condition where plots were established: (D) Total-destruction, (E) blow-down, (F) standing-dead, and (G) old-growth plots.

Table 1. List of plant species present in Chaitén Volcano and their frequency in the big plot and in 20 plots of 4.71 m² in the different studied areas.

| Families | Species | Old-Growth | Standing-Dead | Blow-Down | Near Crater |
|-------------------------------|--------------------------------------|------------|---------------|-----------|-------------|
| SEEDLINGS | | | | | |
| Cunoneaceae | <i>Weinmannia trichosperma</i> | | 2 | | |
| | <i>Caldcluvia paniculata</i> | 4 | 4 | | |
| Eucryphiaceae | <i>Eucryphia cordifolia</i> | 5 | | | |
| Flacourtiaceae | <i>Azara lanceolata</i> | | | 1 | |
| Monimiaceae | <i>Laureliopsis philippiana</i> | 6 | | | |
| Podocarpaceae | <i>Podocarpus saligna</i> | 1 | | | |
| Winteraceae | <i>Drimys winteri</i> | 3 | | | |
| Proteaceae | <i>Embothrium coccineum</i> | | 1 | 4 | |
| | <i>Lomatia ferruginea</i> | 5 | | | |
| | <i>Gevuina avellana</i> | 1 | | | |
| Myrtaceae | <i>Myrceugenia parviflora</i> | 3 | | | |
| | <i>Myrceugenia planipes</i> | 12 | | | |
| | <i>Amomyrtus luma</i> | 16 | 4 | | |
| Araliaceae | <i>Raukiau laetevirens</i> | 3 | | | |
| HERBS AND SMALL SHRUBS | | | | | |
| Gesneraceae | <i>Mitraria coccinea</i> | 8 | | | |
| | <i>Asteranthera ovata</i> | 1 | 1 | | |
| | <i>Campsidium valdivianum</i> | 5 | | | |
| Poaceae | <i>Chusquea uliginosa</i> | 7 | 1 | 1 | |
| Apocinaceae | <i>Elytropus chilensis</i> | 6 | 1 | | |
| Fitolaceae | <i>Ercilla syncarpellata</i> | 3 | | | |
| Saxifragaceae | <i>Ribes magellanicum</i> | | 1 | | |
| Bromeliaceae | <i>Greigia landbeckii</i> | 4 | | | |
| Griselineaceae | <i>Griselinia racemosa</i> | 1 | | | |
| | <i>Griselinia ruscifolia</i> | 4 | 1 | 1 | |
| Gunneraceae | <i>Gunnera tinctoria</i> | | | 1 | |
| Rubiaceae | <i>Nertera granadensis</i> | 1 | | | |
| Hydrangeaceae | <i>Hydrangea serratifolia</i> | 12 | | | |
| Luzuriagaceae | <i>Luzuriaga poliphylla</i> | 8 | 1 | 1 | |
| | <i>Luzuriaga radicans</i> | 14 | | | |
| FERNS | | | | | |
| Dicksoniaceae | <i>Lophosoria quadripinnata</i> | 6 | 4 | 3 | |
| Hymenophyllaceae | <i>Hymenophyllum tortuosum</i> | | | 2 | |
| | <i>Hymenophyllum magellanicum</i> | 2 | | | |
| | <i>Hymenoglossum cruentum</i> | 6 | | | |
| | <i>Hymenophyllum caudiculatum</i> | 3 | | | |
| | <i>Hymenophyllum cuneatum</i> | 2 | | | |
| | <i>Hymenophyllum dentatum</i> | 5 | | | |
| | <i>Hymenophyllum dicranotrichium</i> | 12 | | | |
| | <i>Hymenophyllum krauseanum</i> | 5 | | | |
| | <i>Hymenophyllum pectinatum</i> | 3 | | | |
| | <i>Hymenophyllum plicatum</i> | 3 | | | |
| | <i>Serpilopsis caespitosa</i> | 5 | | | |
| Aspleniaceae | <i>Asplenium daeroides</i> | 4 | | | |
| | <i>Pleurosorus papaverifolius</i> | 4 | | 3 | |
| Dryopteridaceae | <i>Megalastrum spectabile</i> | 7 | | | |
| Blechnaceae | <i>Blechnum mochaenum</i> | 1 | | | |
| | <i>Blechnum arcuatum</i> | 1 | | | |

Table 1. Cont.

| Families | Species | Old-Growth | Standing-Dead | Blow-Down | Near Crater |
|----------------------|------------------------------|------------|---------------|-----------|-------------|
| Dennstaedtiaceae | <i>Blechnum chilense</i> | 2 | 1 | 1 | |
| | <i>Blechnum magellanicum</i> | 1 | | | |
| | <i>Hypolepis rugosula</i> | | | 1 | |
| Total general | | 201 | 22 | 20 | 0 |

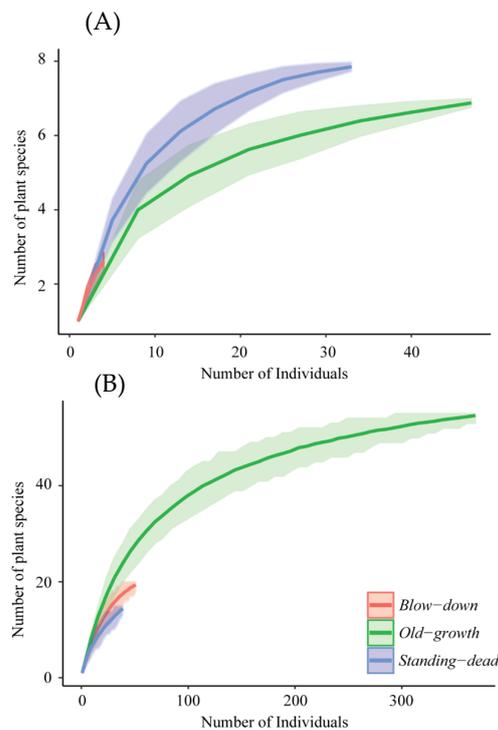


Figure 3. Rarefaction analysis shows the relationship between the number of tree seedling species (A) and small vascular plant species (B) as a function of the number of individuals. In both panels, the shaded area indicates one standard error. All sites affected by the eruption of Chaitén old-growth, standing-dead, and blow-down plots are compared, except for the total-destruction plot, which was not included because of the absence of plants.

Plant composition among old-growth and standing-dead plots showed some similarities (34%) but was less related to the blow-down (20%) and the total-destruction plots (0%). The standing-dead and blow-down plots showed the highest similarities in species composition (Table 2). In the disturbed plots, the recorded plant species were a subgroup of the species present in the old-growth forest plot (Nestedness calculator $T = 13.85^\circ$). The most frequent plant was the fern *L. quadripinnata*, which survived the direct impact of the eruption in small clumps of organic matter that were protected by trunks or the root disc of trees and were not completely covered by tephra. Bamboo and ferns were sprouting from roots in the remnants of exposed forest soil.

Table 2. Sørensen similarity index for the plant composition among the different sites in the Chaitén influence area.

| Site | Old-Growth | Standing-Dead | Blow-Down | Total-Destruction |
|-------------------|------------|---------------|-----------|-------------------|
| Old-growth | 1 | | | |
| Standing-dead | 0.342 | 1 | | |
| Blow-down | 0.2 | 0.526 | 1 | |
| Total-destruction | 0 | 0 | 0.1 | 1 |

3.3. Forest Structure

The forest structure of the old-growth site showed individuals of all sizes, with several large emergent trees (Figure 4). Most trees in the old-growth plot were alive, and the snags most probably represent trees that died before the eruption, while in the other plots, most trees were killed by the eruption. The standing-dead plot showed a similar dbh distribution to the old-growth plot, with a higher frequency of small dbh. The blow-down plot showed a very small number of standing trees, concentrated in the intermediate size class, while the total-destruction plot practically had no individual standing trees (Figure 4).

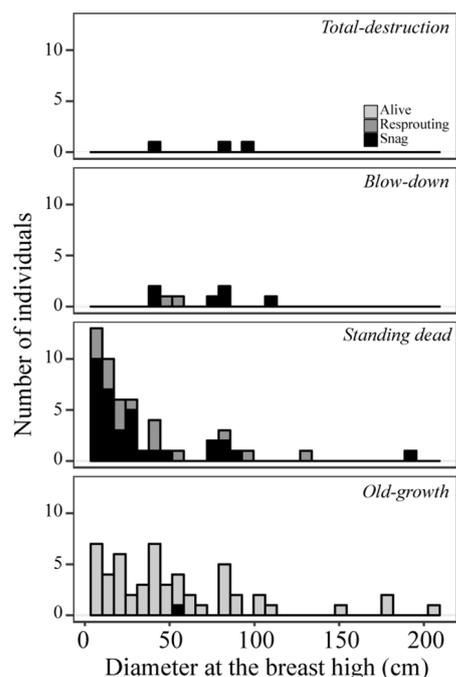


Figure 4. Diameter at the breast height (dbh) distribution for living and standing-dead trees in the study sites. Each panel represents a plot condition influenced by the eruption of Chaitén Volcano.

The basal area of the old-growth plot was dominated by *L. philippiana*, followed by *E. cordifolia* and *C. paniculata* (Table 3). In the standing-dead and blow-down plots *W. trichosperma* and *N. dombeyi* were the dominant components of the basal area, but also with a high number of unidentified trees (Table 3). We were not able to identify the species of the standing-dead trees in the total-destruction plot. The volume of fallen trees increased in the blow-down and standing-dead plots, but it was much lower in the old-growth and the total-destruction plots (Figure 5). In the total-destruction plot, most logs were heavily buried by a dense tephra layer.

Table 3. Total basal area (m²) of tree species in the studied plots: Total-destruction, blow-down, standing-dead, and old-growth. Trees within plots were classified as alive, resprouting after the eruption, or snag when corresponding.

| | Total-Destruction Snag | Blow-Down Snag Resprouting | Standing-Dead Snag Resprouting | Old-Growth Snag Alive |
|------------------------------|---------------------------|----------------------------------|--------------------------------------|-----------------------------|
| <i>Amomyrtus luma</i> | | | 0.02 | 0.34 |
| <i>Amomyrtus meli</i> | | | | 0.06 |
| <i>Caldcluvia paniculata</i> | | | | 2.54 |
| <i>Drimys winterii</i> | | | 0.14 | |
| <i>Lomatia ferruginea</i> | | | 0.04 | 0.01 |
| <i>Myrceugenia planipes</i> | | | | 0.84 |

Table 3. Cont.

| | Total-Destruction | | Blow-Down | | Standing-Dead | | Old-Growth | |
|---------------------------------|-------------------|--|-------------|-------------|---------------|-------------|-------------|--------------|
| | Snag | | Snag | Resprouting | Snag | Resprouting | Snag | Alive |
| <i>Eucryphia cordifolia</i> | | | 0.55 | | 0.59 | 0.61 | 0.26 | 6.37 |
| <i>Laureliopsis philippiana</i> | | | 0.25 | | 0.87 | | | 9.64 |
| <i>Nothofagus dombeyi</i> | | | | | 3.46 | | | |
| <i>Weinmannia trichosperma</i> | | | 0.95 | 0.41 | | 2.38 | | 0.71 |
| <i>Not identified</i> | 1.41 | | 0.94 | | 1.45 | | | |
| Total | 1.41 | | 2.69 | 0.41 | 6.57 | 3.39 | 0.26 | 20.59 |

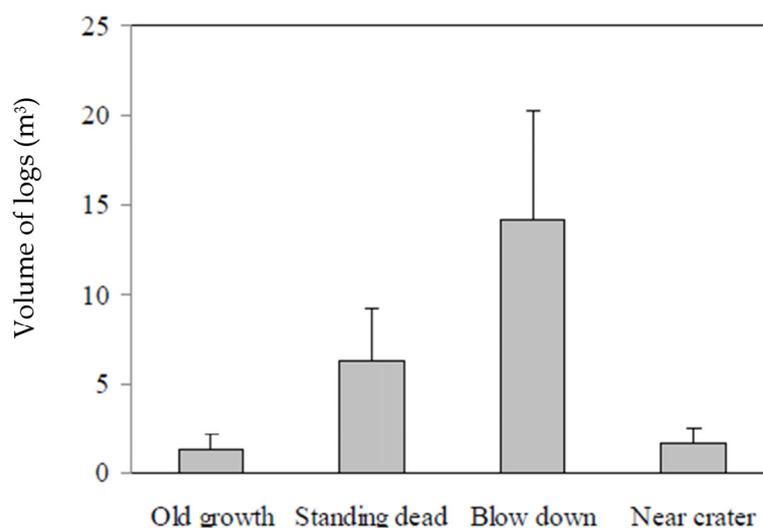


Figure 5. Volume of fallen dead trees (logs) in the study sites influenced by the eruption of Chaitén Volcano in the study sites.

3.4. Seedlings and Small Plants

We found a total of 90 seedlings from five trees and shrub species in the disturbed plots, while we registered 174 seedlings of 12 species in the old-growth plots. The standing-dead plots had 83 seedlings from five species, while the blow-down plots presented 7 seedlings from two species. We did not find any seedlings in the total-destruction plot. In the old-growth plots, seedlings were largely dominated by the shade-tolerant *A. luma*, *M. parviflora*, and *M. planipes*. In the standing-dead plots, seedlings were dominated by *C. paniculata* (48% of the total), but also present were the shade-tolerant tree *A. luma* (24%), and the pioneer tree species *W. trichosperma* and *E. coccineum* (18% and 8% respectively). In the blow-down plot, *E. coccineum*, a pioneer species, and *A. lanceolata* were the only recorded species.

We found different mechanisms of forest regeneration in the plots. In the old-growth plot, most regeneration was from seeds, while in the standing-dead plots, most regeneration came from resprouts and a few tree seedlings from seeds (Table 4). In the old-growth plots, most of the tree seedlings corresponded to species with fleshy fruits dispersed by birds, while in the standing-dead plots, most seeds were wind-dispersed. In the blow-down plots, all seedlings came from seeds (Table 4), but half of the seedlings corresponded to species dispersed by birds (e.g., *Ribes magellanicum*), and the other half were species dispersed by wind (e.g., *E. coccineum*). Second, in all plots, most seedlings were growing on organic substrata (Table 4), such as organic soil on the ground, root discs, and logs, while few seedlings were growing directly either on the tephra or on rocks. In the blow-down plot, we found 7 seedlings of *E. coccineum* growing just in remnants of organic litter; in the standing-dead plot, 11 seedlings were growing directly in the tephra; while the other

72 seedlings were resprouting directly from the standing tree's trunks. In the old-growth plots, we found just one species growing in an exposed rock while the rest of the seedlings were growing in organic substrates (Table 4).

Table 4. Number of seedlings per regeneration type and substratum type in the plots.

| | Regeneration Type | | Substratum Type | |
|-------------------|-------------------|------|-----------------|---------|
| | Resprouting | Seed | Mineral | Organic |
| Total-destruction | - | - | - | - |
| Blow-down | - | 7 | - | 7 |
| Standing-dead | 74 | 9 | 11 | 72 |
| Old-growth | 31 | 127 | 1 | 157 |

Other small plant species in the plots studied (Table 1) showed differences along the disturbance gradient (Table 2). For example, the old-growth plot has species in all categories of plant cover, with few species covering over 75% of the ground and many species covering between 1–5% (Figure 6). In contrast, standing-dead and blow-down plots were covered by fewer species and concentrated in the lower ranges of coverage (Figure 6). In the total-destruction plot, we only found a non-vascular plant (*Marchantia* sp.) with a cover between 5–25% (Figure 6) growing on a log exposed to the surface. The dominant understory species in the old-growth forest were the bamboo *Chusquea* spp. and the fern *L. quadripinnata*. These species were also present in the standing-dead and blow-down plots, although they were scattered and with a low percent of coverage in the disturbed plots.

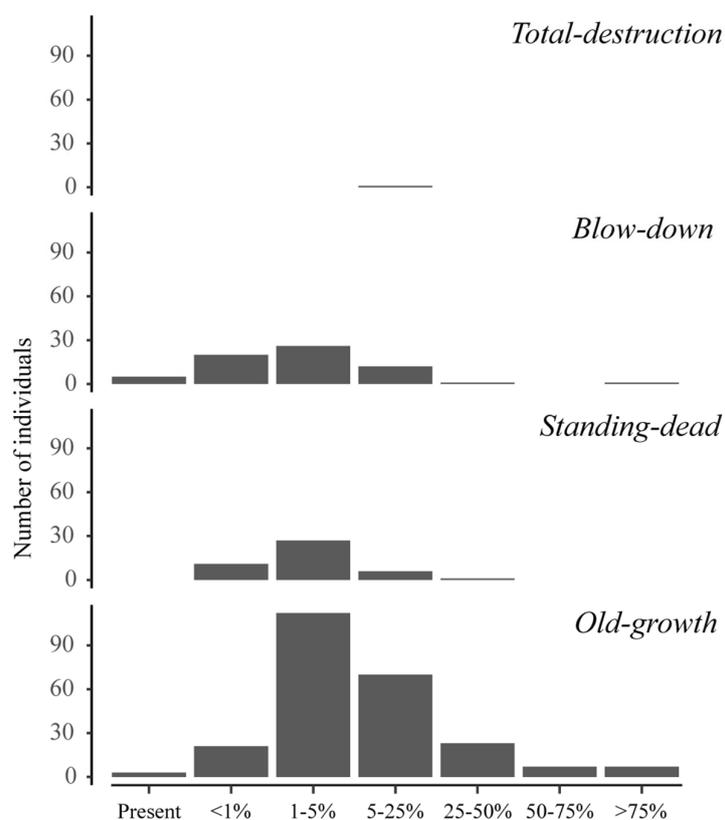


Figure 6. Number of individuals or colonies per relative coverage range at the ground level of the study areas affected by Chaitén Volcano, including vascular and non-vascular species. Panels correspond to the plots distributed in the different disturbance zones.

4. Discussion

4.1. The Relevance of Biological Legacies

Few studies have been conducted shortly after an eruption in the southern Andes; however, successional models predict that disturbed areas in low- and mid-altitude (<1000 m a.s.l.) forests would be dominated by *Nothofagus* species due to shade intolerance, e.g., [38]. In the present study, one year after the eruption, we did not register the *Nothofagus* species despite their abundance in the surrounding undisturbed areas. It is worth noting that the *Nothofagus* species have a cyclic seed production [39,40], which could have resulted in low seed dispersal in the preceding year, although due to the short-term and limited spatial extension of this study, we were unable to confirm this. However, our results suggest that regeneration in the blast zone occurs mainly due to the in situ development of plants associated with biological legacies such as logs, organic soil clumps, and individuals that survive the eruption. Other areas disturbed by Chaitén Volcano presented similar types and abundance of biological structures as well [1].

Similar patterns have been documented in other volcanic regions, too. For instance, studies on Mount St. Helens in the United States revealed that surviving vegetation and organic matter played pivotal roles in ecosystem recovery following the 1980 eruption. Franklin and collaborators [41] emphasized that biological legacies (including surviving plants and organic debris) provided critical refugia and sources for recolonization. This aligns with findings from the Chaitén and Calbuco volcanos in Chile [42], where the presence of biological legacies facilitated resprouting and regeneration.

However, the significance of biological legacies can vary depending on the eruption's intensity and the ecosystem's resilience. In some cases, severe eruptions may obliterate all organic matter and the biological legacies it provides, necessitating primary succession processes. For example, the 2008 eruption of Kasatochi Island in Alaska resulted in the complete removal of pre-existing vegetation and soil, leading to a primary succession dominated by colonizing species, e.g., [43]. This contrasts with Chaitén, where the preservation of biological legacies enabled, in some areas, secondary succession through resprouting. As volcanic eruptions are highly variable, this study, like others, underlines [44,45] the importance of identifying the disturbance type and its internal variability to understand successional processes.

4.2. Resprouting and Seed Dispersal Mechanism

The initial establishment of tree species, besides the disturbance gradient, may be influenced by the interaction between the life history of the species and the altitudinal gradient. Life history attributes, such as seed dispersal, flowering phenology, growth form, resprouting ability, or light-temperature stress resistance, are all mechanisms that influence the recovery response of post-disturbance vegetation [46–50]. In the disturbed plots, the principal regeneration mechanism was the resprouting capability of species (Tables 1 and 4). This is a frequent strategy in many plant species in response to disturbances of different types and intensities [51,52].

Seed dispersion syndrome is another important mechanism that influences colonization after disturbance. Valdivian temperate rainforests have one of the highest proportions of plants dispersed by frugivorous birds when compared to other temperate rainforests [53,54]. Birds consume a high proportion of fruits and may disperse seeds to specific places, such as to a perch [55,56]. Seed availability might increase in sites where remnant snags, shrubs, or perching trees are available, e.g., [57]. Among the wind-dispersed seeds, we only found seedlings of *E. coccineum* in disturbed plots. While this tree has adapted to stressful conditions, the seed is able to disperse for long distances [58].

The importance of animal-mediated seed dispersal in post-eruption recovery has been observed in other contexts than in Chaitén. On Surtsey Island, Iceland, birds contributed to the spread of plant species by transporting seeds, enhancing plant colonization rates [59]. Similarly, studies on Mount St. Helens reported that birds and mammals facilitated seed dispersal, aiding vegetation recovery [60]. Evidence from past volcanic disturbance (Sollipulli-Alpehúe, ~3 ka BP) suggests that in semi-arid conditions, zoochory might play an important role, as well, in the spread of *Ephedra* after burying a huge area into the steppe [44].

On the contrary, in other volcanic landscapes, wind-dispersed species played a more prominent role in early succession. For instance, following the eruption of Mount Usu in Japan, wind-dispersed herbaceous species rapidly colonized the volcanic deposits, initiating succession processes [61]. This suggests that the relative importance of seed dispersal mechanisms can vary based on species traits and environmental conditions.

4.3. Environmental Gradients and Recovery

For tree species, the standing-dead plot had more species than the old-growth plot, while the reverse was true for non-tree species, revealing the effect of the eruption on the small plant species. In the blow-down and total-destruction plots, i.e., from mid to high disturbance intensity at mid to high altitudes and without/or sparse biological legacies, we found low species richness and coverage and sparse tree regeneration. This mosaic of legacies in the landscape offers opportunities for the recolonization of many different species in the affected area. The different species compositions would promote different pathways to early succession with different communities but also to different recovery rates. We propose that in low- to mid-elevation areas of Chaitén Volcano, the vegetation recovery will be faster, dominated by species that are shade-tolerant to semi-tolerant and dispersed by birds, aided by corresponding biological legacies. However, we can expect that at higher altitudes, vegetation recovery would be slower (due, in part, to lower temperatures) with recolonization made by shade-intolerant plants whose seed is dispersed by winds.

Environmental gradients, such as altitude and disturbance intensity, are well-known to influence successional trajectories. Research on Mount St. Helens demonstrated that elevation and disturbance severely affected species composition and recovery rates, with lower elevations supporting more rapid vegetation establishment [60]. Similarly, studies in Hawaii's volcanic landscapes revealed that soil development and nutrient availability along altitudinal gradients significantly impacted plant succession [62]. However, the interplay between environmental gradients and succession is complex and context-dependent. In some cases, higher elevations may experience faster recovery due to favorable microclimatic conditions or proximity to seed sources. For example, research on the 1977–1978 eruptions of Mount Usu indicated that certain high-altitude areas exhibited rapid colonization by pioneer species, which were facilitated by wind dispersal and suitable substrates [61]. Our study further highlights the need to consider local factors when assessing successional dynamics across environmental gradients.

5. Conclusions

The 2008 eruption of Chaitén Volcano provided a unique opportunity to study ecological succession in response to volcanic disturbances. The primary findings from this study highlight the critical role of biological legacies and resprouting in early vegetation recovery in the Andean temperate forests.

This study observed that areas near the crater exhibited high devastation, with no surviving species or tree regeneration after the first year. In contrast, less affected zones permitted the resprouting of damaged trees and the regeneration of small plants and seedlings.

This pattern underscores the importance of biological legacies—such as surviving plant material and organic substrates—in facilitating ecosystem recovery. In the blast zone of the volcano, resprouting from trunks and buried roots emerged as the dominant regeneration strategy, while seedling establishment was limited.

This study highlights the role of frugivorous birds in seed dispersal, facilitated by remnant structures such as snags and perches. This interaction may be promoting the establishment of fleshy-fruited species in disturbed areas. In contrast, wind-dispersed species were less prevalent, except for certain (unexpected) pioneer species that had adapted to stressful conditions.

Vegetation recovery was faster in low-altitude, less-disturbed areas dominated by shade- and semi-tolerant species, while higher altitudes and severely disturbed zones exhibited slower recovery—colonization by shade-intolerant and wind-dispersed species was more important under this condition, although scarce.

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