Vegetation dynamics under residual large trees following a volcanic eruption in a Valdivian temperate rainforest

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Abstract Airborne volcanic ejecta (tephra) can strongly influence forest ecosystems through initial disturbance processes and subsequent ecological response. Within a tephra-disturbed forest, large trees may promote plant growth and create favorable sites for colonization. Three primary ways trees can influence posteruption vegetation response include: (1) amelioration of volcanic substrates, (2) providing source propagules from the tree or from associated epiphytes, and (3) sheltering understory vegetation, thereby increasing the rate of recovery near tree bases. Here, we evaluate Valdivian temperate rainforest understory vegetation responses in close proximity to large trees that survived the 2015 eruption of Calbuco Volcano. Understory vegetative cover was higher near the base of trees for mosses, many epiphytes, and some herbaceous, shrub, and trees species. However, significant interactions with year of measurement, and individualistic responses by many species made generalizations more difficult. Shrubs and trees in particular demonstrated patterns of recovery that were frequently independent of distance. In some cases, percent cover of colonizing vegetation actually increased away from trees by 2019. The soil surface was similarly variable where bare soil cover was associated with locations proximal to tree bases, but material shed from living and dead standing vegetation increased wood and litter abundances on the soil surface away from the base of trees. Soils near trees had lower pH, elevated organic matter, and higher nitrogen and carbon. Our results support the assertion that in this temperate rainforest ecosystem large trees may provide important early refugia for vegetative regrowth following a tephra-fall event with altered edaphic conditions. Nevertheless, individualistic dynamics of different species and growth forms suggest the influence of large trees on nearby understory plants is more complex than a simple facilitative model might suggest.

Keywords Calbuco Volcano · Chile · Patagonia · Tephra · Disturbance ecology · Vegetation

Communicated by Christopher Carcaillet.

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Introduction

Patterns of plant succession following disturbance, including volcanic disturbance, remain fundamental in ecology (Walker and Wardle 2014; Meiners et al. 2015; Chang et al. 2019). Burial by tephra (aerially deposited volcanic ejecta) represents the most widespread form of volcanic disturbance worldwide, and can impart a significant and lasting influence on vegetation (Ayris and Delmelle 2012). Nevertheless, recovery dynamics in areas disturbed by volcanic tephra are not fully understood (Cook and Halpern 2018; Chang et al. 2019; Zobel and Antos 2017; Fischer et al. 2019). In the last decade, multiple volcanic eruptions have resulted in tephra deposition events in Valdivian temperate rainforests in Chilean Patagonia (Castruccio et al. 2016). Postdisturbance vegetation dynamics have been described in these forests after disturbances by tree-fall gaps (González et al. 2015), catastrophic mass movements (Veblen and Ashton 1978), and volcanic eruption (Kilian et al. 2006), but less-so with respect to the impact of tephra deposition on plant community dynamics (Swanson et al. 2016). The recent eruptions provide an opportunity for real-time measurement of vegetation response to volcanic disturbance that have previously been more widely studied in northern hemisphere ecosystems (especially Mount St. Helens, USA) (Crisafulli et al. 2005, 2015; del Moral 2010; Walker et al. 2013; Magnússon et al. 2014; Chang et al. 2019).

Tephra effects on ecosystems depend on the variety of abiotic and biotic factors: tephra characteristics (e.g., texture, particle mass, deposit thickness, and chemistry); secondary disturbances (e.g., erosion and deposition); timing of the event (e.g., season, time of day); topography, aspect, and slope gradient of the sites affected; and the characteristics of the vegetation at the time of disturbance. For example, vegetation may be damaged by dense tephra with coarse grain size and abrasive surfaces (Swanson et al. 2016), whereas fine-grained, low density tephra falling in ecosystems adapted to frequent burial (e.g., by heavy snowfall) may have a variety of influences depending on site conditions (Fischer et al. 2019), or even a positive long-term influence on forest growth (Griggs et al. 1919; Miller et al. 2012). Residual understory vegetation, falling branches and foliage, epiphytes, animal carcasses, and soil collected in axils may interact with tephra deposition to influence ecosystem responses to disturbance. Given the large number of factors that can influence plant responses to tephra fall, it is important to conduct research at individual sites and microsites through time to assess patterns of vegetation change. Measurement of individual sites through time is also essential to distinguish changes in vegetative cover for surviving individuals versus recruitment of new individuals in individual microsites (Zobel and Antos 2009).

Large trees can modify microsite and substate condition during tephra deposition and therefore influence posteruption vegetation dynamic. The zone of influence of forest canopies on ecosystems has attracted the attention of researchers for several decades (e.g., Zinke 1962, Veblen and Ashton 1978; Binkley and Giardina 1998, Bigelow and Canham 2017, Van Nuland et al. 2017), however, no study that we are aware of has addressed the role of extant trees (live or dead) in structuring posttephra deposition vegetation dynamics. Forest vegetation type influences ecosystem level response to disturbance (Turner et al. 1998; Lindig-Cisneros et al. 2006; Gil-Solórzano et al. 2009; Chang et al. 2019; Fischer et al. 2019), and the presence of biological legacies is fundamental to responses in forest ecosystems (Franklin and Halpern 1989; Franklin 1990; Foster et al. 1998; Crisafulli et al. 2005; Cook and Halpern 2018). In addition, soil organic matter content can be an important correlate with ecosystem response (Gil-Solórzano et al. 2009), and may increase with proximity to biological legacy trees. Plant recovery can be especially limited by nutrient content in newly deposited volcanic substrates (Del Moral and Grishin 1999; Halvorson et al. 2005). Accordingly, ecosystems that receive thick deposits of abrasive, high-density tephra may see a heightened influence of individual tree canopies on recovering vegetation due to organic matter contributions to the forest floor. The influence of tree canopies may be consistent with the concept of islands of fertility where surviving trees create unique substrate conditions that facilitate other plant species (Callaway 1995, 2007; Bonanomi et al. 2008): first, higher amounts of organic matter are deposited under trees during or after a scouring tephra-fall event (where vegetation and canopy soil is scoured from the trees and is disproportionally more abundant near the base of trees); second, the shedding of dead and dying material (bark sloughing and recruitment of branch structures from the canopy) during the first few

posteruption years can also contribute large amounts of organic matter; and third, faster regrowth and subsequent litter may then be contributed to the soil environment under the tree canopy. After an intense disturbance event, surviving trees may also provide both a source of propagules and a sheltered site for germination and establishment of colonizing species, thereby affecting colonization rates and species composition (Bruno et al. 2003). Similarly, surviving trees may ameliorate posteruption environmental conditions by providing shade, collecting, and concentrating water (via stemflow and condensation surfaces), and reducing soil moisture stress. These facilitative mechanisms may be stronger in high-stress environments, such as those experiencing frequent and high intensity disturbance (Bertness and Callaway 1994).

Here, we use three years of fine-scale observations focused on areas adjacent to large surviving trees to evaluate posteruption dynamics of understory species following the 2015 eruption of Calbuco Volcano in the southern Chilean Andes. We hypothesized that proximity to large trees would positively influence residual plants and colonizing seedlings. Accordingly, we expected community differences based on proximity to large trees and through time as communities recovered in the immediate years following the eruption. Based on the initial observation of high amounts of canopy detritus near the base of tree boles, we further hypothesized correlations between surface soil edaphic variables and plant responses. We expected that nutrient and organic matter (OM) levels of the soil adjacent to tree bases would also be greater than at nonadjacent sites.

Methods

Study site

Our research was conducted on the north flank of Calbuco Volcano in the Andes Mountains of the Los Lagos region of southern Chile, 30 km east of the city of Puerto Montt at Parque Volcánico Valle los Ulmos (Latitude − 41.296, Longitude − 72.589). The park is a private 650 hectare conservation and environmental education center established in 2013. The area is dominated by Valdivian evergreen temperate rainforest (Veblen and Ashton 1978; González et al. 2015) that is contiguous with Llanquihue National Reserve

(33,974 hectares) to the south and east. Both our study area and Llanquihue National Reserve lie within the broader Valdivian rainforests of southern Chile Biosphere Reserve (UNESCO 2011). Over the 2015–2019 period, annual precipitation ranged from 1644 to 2282 mm based on the TerraClimate global climate model (Abatzoglou et al. 2018; http://www.climatologylab.org/terraclimate.html last accessed Dec. 26, 2020). Precipitation is unevenly distributed throughout the year with greater precipitation in fall and winter months. The average monthly minimum and maximum temperature are approximately 1.8 and 11.45° C, respectively, based on the data available from 2015 to 2019 (Abatzoglou et al. 2018).

Calbuco is an active stratovolcano that underwent a series of energetic explosive eruptions during April 2015 (Romero et al. 2016). At our study site, on the north slope of the mountain, trees and shrubs were subject to total defoliation, severe branch removal, and burial by up to 43 cm of coarse, primarily basaltic–andesite tephra (scoria), with many perennials surviving the event and re-sprouting the following growing seasons. Branches of both emergent and midstory trees were severely broken, leaving only portions of the largest of branches intact on most trees, reducing them to columnar forms, often with < 3 m canopy radii (Fig. 1).

Forests at the study site were dominated by late succession, shade-tolerant *Laureliopsis philippiana* (Atherospermataceae) and *Dasyphyllum diacanthoides* (Asteraceae), with mixed subcanopy species *Amomyrtus luma* (Myrtaceae) and *Myrceugenia planipes* (Myrtaceae). Other occasional tree or tree-like shrub species that occurred near, but not in, our transects included *Raukaua laetevirens* (Arallaceae), *Weinmannia trichosperma* (Cunoniaceae), *Rhaphithamnus spinosus* (Verbenaceae), *Azara lanceolata* (Salicaceae), and *Myrceugenia chrysocarpa* (Myrtaceae). At slightly higher elevation near the site, tree species *Drimys winteri* (Winteraceae) and *Nothofagus dombeyi* (Nothofagaceae) were also common. Tree stem density averaged 533 stems ha^{-1}, and *L. philippiana* were between 227 and 480 stems ha^{-1} at our sites. The dominant shrub species are *Fuchsia magellanica* (Onagraceae), and *Ribes magellanicum* (Grossulareaceae), and co-occur with *A. luma* and *M. planipes* saplings. Large evergreen bamboos (*Chusquea* spp.; Poaceae) are common in the understory. Common epiphytes are *Mitraria coccinea*

Fig. 1 Defoliated *Laureliopsis phillipianna* canopy trees with limited horizontal canopy width (often < 3 m) following the eruption at Volcán Calbuco in 2015. Photo taken in January 2019, following four years of regrowth. Trees are approximately 30 m in height

(Gesneriaceae)*, Hydrangea serratifolia* (Hydrangeaceae)*,* and *Luzuriaga radicans* (Alstroemeriaceae). A mixed community of fern, lichen, and bryophyte taxa including *Asplenium* spp. (Aspleniaceae)*, Hymenophyllum* spp. (Hymenophyllaceae), and *Marchantia* sp. (Marchantiaceae) occur both as epiphytes and growing on ground surfaces. Within our study site, most of the overstory trees and understory shrubs survived severe damage from the tephra fall, while plants that were shorter than the 26–43 cm thick tephra deposit were buried. However, some of these buried individuals survived, including aforementioned woody species, ferns, and herbaceous taxa (hereafter "herbs"). These species included *Asplenium dareoides, Blechnum blechnoides* (Blechnaceae)*, Hymenophyllum* sp.*, Solidago chilensis* (Asteraceae)*, Uncinia* sp. (Cyperaceae), and *Urtica* sp. (Urticaceae) (see Table 1 for species list). Occasional emergence of

tephra-buried perennial ferns and herbs was observed over 1–4 years posteruption, (sensu Swanson et al. 2016), but this appeared to be a rare phenomenon at our sites, and re-emerging individuals could easily be discerned from colonizing vegetation based on leaf and stem characteristics.

Tree selection

Sixty living representative older *L. philippiana* trees were selected from between 656 and 754 m elevation and within a standardized size range from 65 to 141 cm diameter (DBH; measured 1.37 m above the ground). Trees were haphazardly selected using ten trees evenly distributed in each of six south-to-north 10 m × 150 m belt transects arranged evenly along hill-slope contours over the 98 m elevation gradient.

For each studied tree, DBH, geographic location, and elevation were recorded (average locations were based on > 100 GPS points; WGS 84; Garmin Oregon 550t GPS, Garmin International, Inc., Olathe, KS, USA). A transect azimuth for understory recovery measurement was randomly selected for each tree. Transects were 3 m long, originating from the base of each tree, moving outwards. Transect length was determined in the field based on remnant canopy radii such that the transects would extend beyond the extant crown dripline for each tree. In order to control for potential interference by other trees, an azimuth was rejected if the resulting transect ran within 2 m of another tree ≥ 65 cm DBH, within 1 m of another tree < 65 to ≥ 30 cm DBH, or under the crown dripline of another tree. Azimuths crossing over confounding features, such as a downed or uprooted tree, were eliminated and another azimuth was randomly chosen until selection criteria were met.

Vegetation sampling

Vegetation was sampled for three consecutive years beginning in 2017. A 10 cm × 40 cm quadrat frame was used to record cover along sampling transects at near the base of the tree (0 and 20 cm; hereafter "base"), at intermediate distances (50, 90, and 150 cm), and more distant (200, and 270 cm; hereafter "open") from the base of the tree. This small frame size was chosen early on based on the visual surveys of surviving residual and early colonizing vegetation – mostly consisting of small herbaceous and non-

Table 1 Taxa (species or species group) list by growth form with relative dominance (cover) and relative frequency values

Species List by Growth Form	Relative Dominance	Relative Frequency
Epiphytes		
Asplenium dareoides Moritz	**0.228**	**1.883**
Campsidium valdivianum (Phil.) Skottsb	0.022	0.130
Hydrangea serratifolia F.Phil	**25.692**	**15.195**
Hymenophyllaceae Mart	0.044	0.195
Hymenophyllum sp. Sm	0.097	0.390
Luzuriaga radicans Ruiz & Pav	**2.306**	**5.260**
Mitraria coccinea Cav	**3.860**	**2.597**
Shrubs		
Azara lanceolata Hook. f	0.028	0.325
Berberis ilicifolia Hort. ex K.Koch	0.014	0.130
Berberis trigona Kunze ex Poepp. & Endl	0.108	0.195
Berberis sp. L	0.014	0.260
Chusquea **spp.** Kunth	**4.792**	**3.117**
Fuchsia magellanica Lam	**20.986**	**21.818**
Ribes magellanicum Poir	**2.278**	**2.338**
Solanum valdiviense Dunal	**0.939**	**0.519**
Trees		
Amomyrtus luma (Molina) D.Legrand & Kausel	**15.185**	**20.065**
Aristotelia chilensis Stuntz	0.284	0.195
Dasyphyllum diacanthoides (Less.) Cabrera	**2.250**	**0.779**
Laureliopsis philippiana (Looser) Schodde	0.028	0.455
Myrceugenia planipes O.Berg	**10.904**	**17.143**
Herbaceous		
Blechnum **spp.** L	**5.582**	**3.442**
Blechnum blechnoides (Lag.) C.Chr	NA	NA
Blechnum mochaenum G.Kunkel	NA	NA
Hypochaeris radicata L	0.584	0.195
Hypolepis poeppigii (Kunze) R.A.Rodr	**0.770**	**0.325**
Solidago chilensis Meyen	0.029	0.130
Uncinia sp. Pers	0.017	0.065
Urtica **sp.** L	**1.946**	**0.974**

[a]Only species with a combined relative dominance and frequency value of > 1 were used in the species by species analysis (bolded text). All species were used in the growth form analysis regardless of relative dominance or frequency

vascular plants, seedlings, and saplings. Visual cover estimates (cm^2) were made for each species, taxon, moss (grouped), lichen (grouped), liverwort (grouped), as well as for a set of environmental/substrate variables: scoria, bare soil, litter, wood, and standing dead vegetation. Portions of the quadrat occupied by living woody plants with stem or bole diameters $\geq$ 1 cm cover were recorded as a composite 'trunk' cover value. Cover estimates were recorded for all individuals rooted in each plot. All individuals were identified as residuals (individuals persisting from the pre-eruption flora) or colonizers (individuals that colonized from seed, spore, or vegetative propagules posteruption) based on detection of cotyledons, juvenile leaf morphology, or, in some rare cases, careful nondestructive excavation of roots to determine rooting location above vs. below scoria deposits. Cover was estimated separately for residuals and colonizers for all species. All cover estimates used blank 10 cm^2 and 100 cm^2 placards as reference guides to ensure uniformity.

Vegetation was classified into growth form for analysis based on the dominant mature form and habitat observed at the site. We grouped vegetation

into the following growth form categories: Mosses, Liverworts, and Lichens (nonvascular plants and lichens that were found both on tree bases and branches, and on ground surface), Epiphytes (vascular plants typically found growing on trunks and branches of live trees but also on ground surface), Shrubs (primarily growing as small woody growth forms less than 3 m tall without clear central growth axis), Trees (growing as small to large woody trees with central apical growth habit), and Herbaceous plants (non-woody growth forms found primarily growing on the ground).

Soil sampling

For each study tree, we sampled soil composition (< 2 mm fraction) to assay pH, organic matter (OM), carbon, and nitrogen content. Soils were collected in 2017 at the base of the tree bole (n = 60; hereafter referred to as 0 cm) as well as at a randomly selected subset of canopy interspaces (n = 18) at 290–300 cm on the transect with care taken to sample > 20 cm distant (perpendicular) from the transect line to minimize disturbance. Samples of ~ 10 cm^3 were extracted as square cube of substrate using a hand trowel. Samples were immediately air-dried for 72 h (~ 21 °C), and then stored in plastic bags until analysis. Subsamples were weighed to determine the ratio of air-dry mass to oven dry mass (dried at 105 °C for 72 h) immediately prior to further analysis. Total OM was determined on the < 2 mm sieved size fractions through loss on ignition ash free dry mass where 10 g subsamples of each dried soil sample were combusted for 5 h at 500 °C in a muffle furnace. Finally, 5–10 mg air-dried subsamples of < 2 mm material from each soil sample were also analyzed for total C and N content using a Perkin-Elmer 2400 Series II CHNS/O Elemental Analyzer (PerkinElmer Inc., Branford, Connecticut, USA). Average bulk density was calculated based on the weight to volume ratio for the < 2 mm fraction of bulk substrate sampled as described above. All values of % OM, C, and N were also multiplied by bulk density and depth of sample to estimate OM, C and N on a mass per area basis. All samples were weighed to the nearest 0.001 g.

Statistical analyses

Analysis of patterns in both residual and colonizing plant species was conducted by growth form, and by individual species (or taxon). For our individual species analysis, we included only those species with a value of ≥ 1.0 combined relative dominance (relative cover) and relative frequency score (see Table 1). Relative dominance was calculated as the total cover of a given species in all plots divided by the combined cover of all species in all plots, multiplied by 100. Similarly, relative frequency was calculated as the total number of plots with occurrence of a given species divided by the number of plots measured, multiplied by 100. All species were included in analyses by growth form regardless of relative dominance or frequency. In two genera, *Chusquea* and *Blechnum*, multiple species were lumped within genus for analysis because of the difficulty in distinguishing species among juvenile and newly emerging individuals. For our focal tree species, *L. philippiana*, only woody portions of trees were present in the data for only a few plots. There were no seedlings or saplings of this species. Accordingly, this species was not included in our calculations of relative dominance or frequency.

Data were combined into the three distance categories (base, intermediate, and open) for analysis reflecting different distances from the base of trees. Species and growth form data were also centered relative to highest values prior to analysis, and log-transformed (Log(1 + x)) when non-normal. To analyze the significance of patterns in % cover with distance from tree base through time, we used a REML mixed model approach. Differences in cover within each test were evaluated using distance from bole and year as categorial fixed effects, and aspect (direction from tree), and individual sample location nested within tree ID as random effects. Distance from tree base was treated as a categorical fixed effect (as described above) so as to allow for the possibility of nonlinear responses with distance from tree base. All models were run, and parameters estimated, using the *lme4* and *LmerTest* packages in R (Bates et al. 2015; R Core Team 2019). Because conducting multiple analyses on the same dependent variable increases the chance of committing a Type I error, we conservatively used a Bonferroni correction altered *P* value cutoff accounting for the number of models tested

within each plant growth form in each case where the same dependent variable was used. Post hoc paired contrasts following significant models were conducted using the *emmeans* package *v* 1.6.0 in R.

Community analysis was conducted to determine differences in community profile associated with year and distance relative to the tree bole, and correlations with substrate variables and species. Analyses were conducted with R using the *vegan* package (Oksanen et al. 2016; R Development Core Team 2019). Nonmetric Multidimensional Scaling Ordination (NMDS) was used to visualize the ordination using a Bray–Curtis distance measure. NMDS ordination (based on the ranked dissimilarity matrix), represents multivariate data on two- or three-dimensional axes such that similar communities appear closer together. Statistical differences among groups were evaluated using nonparametric permutational multiple analyses of variance (PerMANOVA) with Bray–Curtis Distance measures, and 1000 permutations (Anderson 2001). Vectors for correlations between community ordinations and species abundance and substrate data were conducted using *envfit* function in *vegan* (Oksanen et al. 2016). Vectors represent correlations of environmental (biotic or abiotic) variables with the ordination (r^2) and are graphically portrayed on the ordination where length is proportional to r^2, and direction represents the relative influence each given variable plotted from the overall data centroid in ordination space. Centroids (averages) of data within each year and distance category were used to graphically represent results in NMDS ordinations with vectors from plot-level analysis.

Analysis of surface substrate (percent cover of bare soil, litter, or woody material in plots) versus distance from the base of trees and year was conducted using a REML approach (as above; distance from bole and year treated as categorial fixed effects and aspect and individual sample location nested within tree ID as random effects) followed by paired contrasts for multiple comparisons using the *emmeans* package *v* 1.6.0 in R. To determine statistical differences in the soil N, C, OM, and pH, where data was sampled in a single year (2017) adjacent to tree boles and under canopy interspaces only, we used simple Welch's t–tests comparing tree base and 3 m distances from each tree. As above, analyses were conducted using R (v. 3.6.1), and an α value of 0.05 was used to denote significance.

Results

Plant growth form

When taxa were grouped and analyzed by growth form, several clear patterns emerged (Supplementary Table 1, Fig. 2). Consistent with our original hypothesis, combined residual lichen and bryophyte cover were higher near the base of trees ($\sim$ 9–13%, $P < 0.001$) than at intermediate and open sites ($< 5\%$ cover) in all years ($P < 0.001$) driven by differences in moss (Supplementary Tables 1 and 2). A significant distance by year interaction ($P = 0.002$) was a result of stronger patterns in 2018 and 2019 when moss was 13.2%, and 11.3% cover respectively ($P < 0.001$). Similarly, residual epiphytes declined with distance from tree bases in all years ($P < 0.001$; Fig. 2), but differences among years were insignificant ($P = 0.812$). There was no significant relationship for colonizing epiphytes with distance ($P = 0.066$) or among years ($P = 0.184$). Residual shrub cover significantly decreased through time ($P = 0.003$), but not based on distance ($P = 0.017$; nonsignificant based on the Bonferroni correction). In contrast, colonizing shrub cover increased in 2018 (over 2017 values; $P = 0.001$) and remained higher in 2019 even though any pattern with distance categories was not significant ($P = 0.243$). Residual trees did not vary significantly by distance or year ($P = 0.134$, $P = 0.142$). Colonizing trees in 2019, however, demonstrated increased cover in open locations compared to the tree base (interaction effect $P < 0.001$; contrast $t_{515} = 4.579$, $P < 0.001$). Finally, herbaceous cover was generally absent at intermediate and open sites across all years, while for colonizing species a significant increase in cover occurred in 2019, regardless of distance from the tree base ($P < 0.001$).

Mosses, lichens, and liverworts

Moss declined steeply with distance from tree bases in all years ($P < 0.001$; Supplementary Table 2). Moss abundance also varied slightly from year to year ($P < 0.001$), and an interaction between year and distance suggested a stronger effect of distance in 2018 ($P < 0.001$). On average, moss cover was 9–13% near tree bases, and less than 5% of ground cover at intermediate and open sites. Liverwort responses were variable, and there was no consistent
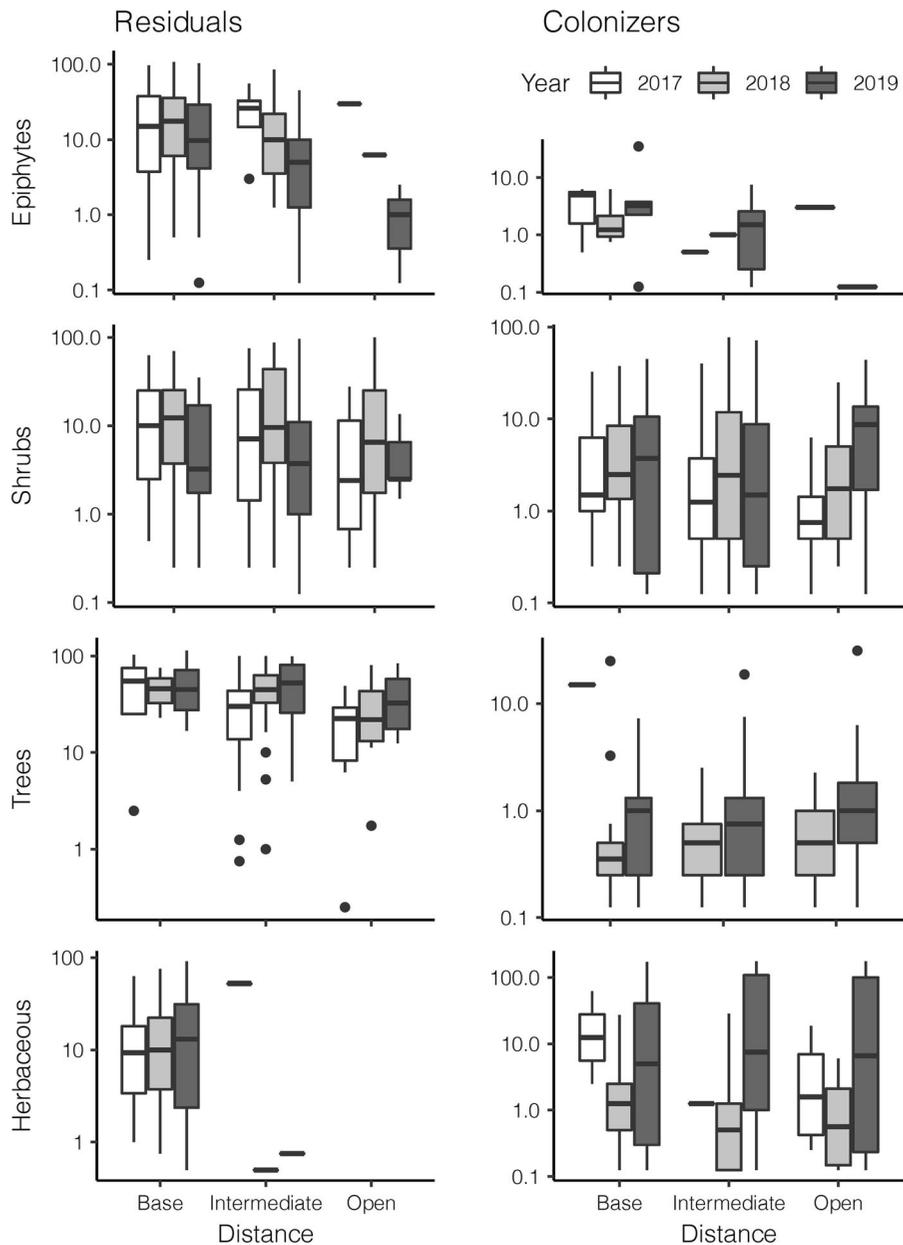
Fig. 2 Box plots of percent (%) cover of plant growth form by distance from tree across all years measured. Colonizers (right panels) and residuals (left panels) are plotted separately with year of measurement represented by differential gray shading.

Single points represent outliers, and solitary horizontal lines (without boxes) represent categories with only a single nonzero measurement. Y axes are plotted on a log scale for ease of visualization

pattern with distance from tree bases ($P = 0.294$) or among years by 2019 ($P = 0.158$), and there was no interaction effect ($P = 0.064$). In contrast, lichen cover was significantly greater in open locations, especially in 2017 and 2018 (distance effect $P < 0.001$; year effect $P = 0.019$; interaction effect $P = 0.013$).

Canopy epiphyte species

Consistent with our original hypothesis, two dominant residual canopy epiphyte species (*Hydrangea serratifolia* and *Luzuriaga radicans*) declined rapidly with distance from the base of surviving trees in all years ($P < 0.001$; Supplementary Table 3). Patterns for residual *Mitraria coccinea*, were not significantly explained by distance ($P = 0.132$). Similarly, there were no statistically significant changes with distance for colonizing *Luzuriaga radicans* or *Asplenium dareoides* ($P = 0.16$, $P = 0.480$; Supplementary Table 3), and there were no other statistically significant patterns in individual epiphyte species responses to year of sampling.

Shrubs and subcanopy tree species

Shrub and subcanopy tree differences among distance categories were variable (Table 2) and frequently inconsistent with our original hypothesis. *Chusquea* spp., a shrubby bamboo, was not significantly different among distance categories or by year. Residual *Fuchsia magellanica* (shrub) demonstrated higher cover near tree bases and increased through time. Another shrub, *Ribes magellanicum*, demonstrated a significant decrease through time in cover of residual plants, but no effect of distance. The residual occasionally vining shrub *Solanum valvidiense* was not related to distance or year of measurement. Residual *Amomyrtus luma* and *Myrceugenia planipes* (trees), also did not demonstrate effects of distance or year, though cover was sometimes higher at intermediate and open sites. Similarly, the tree *Dasyphyllum diacanthoides* did not vary significantly by distance or year.

Colonizing *A. luma* cover was significantly higher at intermediate and open sites after 2018 (Table 2) and increased through time. Colonizing *M. planipes* (subcanopy tree), also increased by 2019. Colonizing *R. magellanicum* was not significantly associated with distance or year. Percent cover of colonizing *F. magellanica* increased after 2017, but this was again not significantly associated with proximity to tree bases.

Herbaceous species

Herbaceous taxa represented a small amount of cover, but exhibited some significant patterns (Supplementary Table 4). *Blechnum* spp. demonstrated both a decline with distance from the tree base ($P = 0.004$), and an increase in the strength of this pattern through time with higher cover values near the base of the tree ($\sim 1.5\%$ in 2017 to $\sim 4\%$ in 2019; distance x year interaction $P = 0.005$). Another residual species, *Hypolepis poeppigii*, showed no significant trends with distance from tree or year ($P = 0.191$, $P = 0.127$ respectively). Among colonizing herbaceous species, *Blechnum* spp. again showed a significant decline with distance from tree bases ($P = 0.006$). *Urtica* spp. showed a significant pattern through time ($P < 0.001$), where average cover increased to $\sim 0.5\%$ by 2019.

Community analysis

Ordination of species-level community data resulted in a two-dimensional NMDS ordination solution with a final stress of 0.19. Ordination of plots by year and distance (Fig. 3) demonstrated trajectories of communities at base, intermediate, and open locations through time where the centroids (community means) for distance categories were also distinct. Slightly higher divergence among locations was clear in 2019. These visual results were supported by our PerMANOVA analysis where distance, year, and the year-by-distance interaction were significant effects, (Distance: $F_{(2, 1275)} = 20.10$, $P < 0.001$; Year: $F_{(1, 1272)} = 52.19$, $P < 0.001$; Interaction: $F_{(2, 1275)} = 3.50$, $P < 0.001$). Distance accounted for 40.4% of the sums of squares for all factors in the model, and year accounted for 52.5%.

All species included in our individual species analysis (see above) represented statistically significant vectors for the ordination. However, only five species had vectors with r^2 values higher than 0.1. The shrub species, *Fuchsia magellanica* ($r^2 = 0.28$) and an herbaceous plant, *Urtica sp.* ($r^2 = 0.18$), exhibited vectors generally aligned with year of measurement (Fig. 3). The tree species *Amomyrtus luma* and *Myrceugenia planipes* ($r^2 = 0.19$ and 0.12, respectively), exhibited vectors roughly aligned with the separations between base to open distance categories. The vector for the epiphyte species *Hydrangea serratifolia* ($r^2 = 0.14$) corresponded with greater

Table 2 Type II ANOVA table from REML model for residual and colonizing tree and shrubs

Source	% ss‡	df	F	P	Significance
Residuals					
Amomyrtus luma					
Year	29.2	2848	1.29	0.275	
Distance	41.7	2210	1.81	0.166	
Year x Distance	29.2	4848	0.67	0.609	
Chusquea spp					
Year	32.1	2848	1.93	0.147	
Distance	10.7	2366	0.57	0.564	
Year x Distance	57.1	4848	1.53	0.189	
Dasyphyllum diacanthoides					
Year	34.1	2848	1.44	0.238	
Distance	30.1	2146	1.27	0.284	
Year x Distance	35.9	4848	0.76	0.554	
Fuchsia magellanica					
Year	35.2	2848	6.04	0.002	*
Distance	36.6	2368	6.29	0.002	*
Year x Distance	28.2	4848	2.43	0.046	
Myrceugenia planipes					
Year	19.2	2848	1.56	0.211	
Distance	14.9	2130	1.21	0.302	
Year x Distance	65.9	4848	2.67	0.031	
Ribes magellanicum					
Year	55.2	2848	7.28	0.001	*
Distance	12.8	2181	1.68	0.189	
Year x Distance	32.0	4848	2.11	0.077	
Solanum valdiviense					
Year	42.9	2848	2.62	0.074	
Distance	22.7	2424	1.37	0.251	
Year x Distance	34.3	4848	1.05	0.382	
Colonizers					
Amomyrtus luma					
Year	66.8	2848	73.68	0.000	*
Distance	14.0	2131	15.47	0.000	*
Year x Distance	19.2	4848	10.59	0.000	*
Myrceugenia planipes					
Year	84.6	2,1081	35.62	0.000	*
Distance	5.3	2115	2.23	0.113	
Year x Distance	10.1	4,1081	2.13	0.075	
Ribes magellanicum					
Year	27.1	2,1272	1.00	0.368	
Distance	2.2	2,1272	0.08	0.924	
Year x Distance	70.7	4,1272	1.307	0.265	
Fuchsia magellanica					
Year	65.9	2745.42	6.03	0.003	*
Distance	17.6	2135.04	1.55	0.215	
Year x Distance	16.4	4845.33	0.72	0.576	

*Significance indicates a significant P value following a Bonferroni correction

‡Percent of total nonresidual component sums of squares represented by each model component

Locations Through Time NMS

Species Vectors NMS
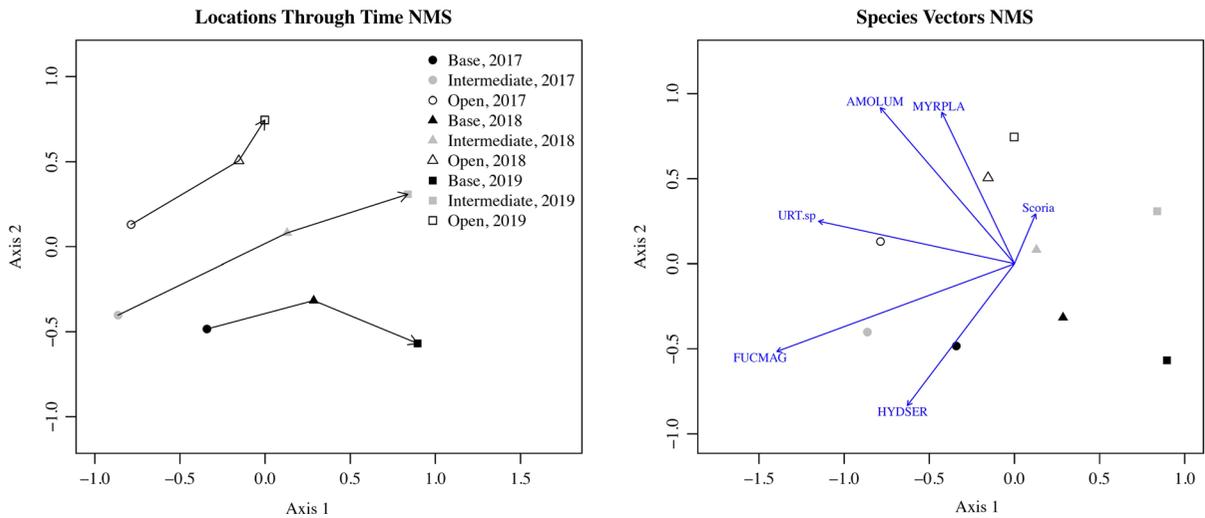
Fig. 3 Nonmetric Multi-Dimensional Scaling ordinations (Bray–Curtis, 100 iterations) of all data grouped by distance category (black, gray, and white) and by year (shapes). Points represent centroids (means) of plot-level ordinations. Ordination stress was 0.19 for multiplot ordination and 0.05 for centroid ordination. Arrowed lines (left panel) between points connect community change through time within each distance

category Vector lines (right panel) represent significant species and substrate correlations with the plot-level ordination with $r^2 > 0.1$. Six-character codes for species represent the epiphyte *Hydrangea serratifolia* (HYDSER), the shrub *Fuchsia magellanica* (FUCMAG), Herbaceous *Urtica* spp. (URT.sp), and the subcanopy trees *Amomyrtus luma* (AMOLUM), and *Myrceugenia planipes* (MYRPLA)

epiphytes near the base of trees, especially in the first year. All growth form vectors were significant, however only three had r^2 values higher than 0.1 (bryophytes, $r^2 = 0.10$, epiphytes $r^2 = 0.21$, and trees $r^2 = 0.28$).

Substrate and soils

Scoria cover increased with distance from the base of the tree with cover values at all distances significantly different from one another ($F_{(2, 424)} = 10.480$, $P < 0.001$; Fig. 4). Scoria cover also declined by 1/3 to 1/2 over the course of the three years of measurements ($F_{(2, 848)} = 188.105$, $P < 0.001$), and each year was also significantly distinct ($P < 0.013$). There was no significant distance category by year interaction. Litter cover approximately doubled between 2017 and 2019 across all distances ($F_{(2, 848)} = 168.528$, $P < 0.001$), and each year was significantly distinct ($P < 0.013$). Litter cover was significantly lower near the base of trees regardless of year ($F_{(2, 424)} = 9.345$, $P = 0.001$), and there was not a significant distance category by year interaction. Year was a significant effect for cover of wood ($F_{(2, 848)} = 14.953$, $P < 0.001$) where it increased by 2019, but was not significantly different between 2017 and 2018. There

was no significant effect of distance on wood cover ($F_{(2, 424)} = 2.365$, $P = 0.095$). Soil cover was higher in all years near the base of trees ($F_{(2, 424)} = 58.598$, $P < 0.001$), but there was no significant effect of year ($F_{(2, 848)} = 0.534$, $P = 0.587$; Fig. 4). When analyzed as vectors in our ordination analysis, both litter and scoria percent cover were significant ($P < 0.001$), however r^2 values were low ($r^2 = 0.01$).

Pearson's correlation analysis for growth forms and the above substrate variables yielded few strong correlations despite similar patterns with distance from the base of trees and general increases in vegetation and organic debris (e.g., litter, wood) through time. Percent cover of bare soil was correlated with residual bryophyte cover and residual epiphyte cover (r = 0.22 and r = 0.24, respectively). Residual epiphytes were negatively correlated with scoria cover (r = -0.20), but less strongly for litter cover (r = -0.14). Bryophytes showed a mild negative correlation with scoria (r = -0.17), and a negative correlation with litter (r = -0.20). All other correlations between growth form categories and substrate cover had r values < 0.1. The epiphyte *Campsidium valdivianum* was significantly correlated with wood (r = 0.13), and the epiphytes *H. serratifolia*, Hymenophyllaceae species, *L. radicans*, and *M. coccinea* were correlated
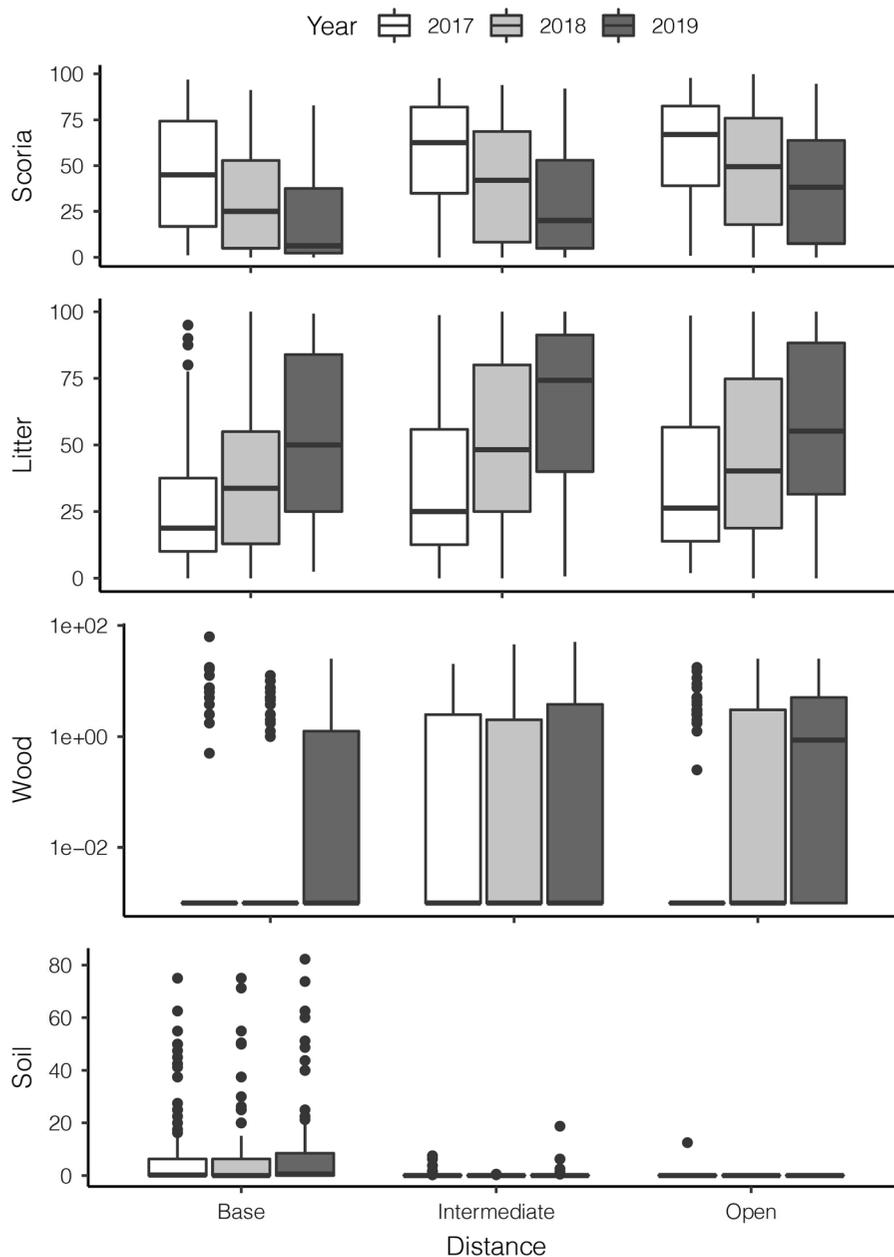
Fig. 4 Box plots of percent (%) cover of substrate by distance from tree across all years measured. Year of measurement is represented by differential gray shading. Single points represent outliers, and horizontal lines (without boxes) represent zero-value medians. Note that for the substrate variable "wood", the Y axis is plotted on a log scale for the ease of visualization

with soil (r = 0.12, r = 0.14, r = 0.15, and r = 0.105 respectively).

In our one-time soil analysis, soil OM at the base of trees was more than five times higher ($P < 0.001$), soil C was more than three times higher ($P < 0.001$), and soil N was more than three times higher ($P < 0.001$)

than at 3 m distances. In contrast, pH was lower (5.07 versus 5.29) adjacent to tree bases than at 3 m distance ($P < 0.001$).

Discussion

Our results suggest vegetation dynamics are variable in proximity to large, surviving trees in the years immediately following a volcanic tephra disturbance event. While we initially hypothesized strong trends in growth, colonization, and community composition with distance from the base of trees, results were more complex. Rather than demonstrating a pattern of uniform positive (facilitative; Bertness and Callaway 1994) or negative (inhibitive; Connell 1983) effects, surviving trees played changing roles depending on the species and growth form and time since the disturbance. Effects were also variable among residual and colonizing (seedling) vegetation. While results for some species may also be consistent with tolerance models of succession (e.g., facilitation, tollerance and inhibitory models of succession sensu Connell and Slatyer 1977), most patterns were variable by species, growth form, and time, rather than simply independent of proximity to surviving trees. Thus, our results were more variable than we expected. Initially, large trees may have played an especially strong role where they may have protected moss, epiphytes, and some shrubs and subcanopy trees from the mechanical damage associated with scouring tephra deposition disturbance. However, as time and vegetation recovery progressed, colonization of new individuals was not clearly enhanced with proximity to large trees. In fact, in some cases colonization was higher away from the base of trees. This may indicate successful colonization beyond the immediate competitive influence (e.g., space, light) of dominant trees, however the short distance of our transects (0–3 m) should encourage cautious interpretation of these data. For epiphyte and moss species though, the influence of large trees as islands of residual survival and abundance was generally consistent across all years. Our ordination analyses supported this growth form-based perspective where distance from tree base was associated with community differences, a key epiphyte species was associated with communities near tree bases, and subcanopy tree species were corelated with community profiles at open sites.

Large trees can affect ecosystem recovery from disturbance (Franklin et al. 2000; Manning et al. 2006; Schlawin and Zahawi 2008; Miao et al. 2013). Studies in other systems (esp. N. hemisphere) have found these biological legacies may drive recovery and successional processes via seed production and dispersal by the surviving species (Turner et al. 1998; Keeton and Franklin 2005) or by surviving individuals providing habitat and perches for seed dispersing birds and mammals (Wunderle 1997; Albornoz et al. 2013). Legacy trees may also provide refugia, protection, or structural support for other remnant or colonizing taxa, especially bryophytes, lichens, and epiphytic ferns and angiosperms (Miao et al. 2013). Additionally, surviving species may influence the structure and chemistry of soils (Zinke 1962; Franklin et al. 2000) leading to changes in plant community composition following disturbance. As suggested by Elmqvist et al. (2001), the influence of large trees in our study may be transient for nonepiphytic species. However, this compounding temporal influence may also be long-lasting due to the process of nucleation (Schlawin and Zahawi 2008), or 'zones of influence' associated with changes in soils (sensu Zinke 1962; see discussion below). While we saw increases in total cover in many of our plots, these increases generally occurred rapidly, and were most apparent in the first and second years of sampling. As such, our data suggest a more complex model where close proximity to large trees is influential on short-term dynamics for some species, and community profiles following disturbance, and soils are predictably richer in OM, C and N near tree bases, but such effects are intertwined with individualistic responses among species.

In Valdivian rainforests, the role of large trees has been explored with regard to canopy gap dynamics (Gutiérrez et al. 2008). Characteristics of treefall gaps (gap area, aspect, species, and size of gap maker, etc.) influence the recruitment of tree species during recovery in Andean montane forests (González et al. 2015). Dominant graminoids represented by *Chusquea* spp. are likely strong competitors in treefall gaps (Gutiérrez et al. 2008), and can inhibit the establishment of seedlings under their canopies (González et al. 2015). Following fire disturbance, Albornoz et al. (2013) found regeneration radiated from surviving individuals that provide seed as well as micro-environments more suitable for propagule deposition and plant survival. In northern hemisphere temperate rainforests with high levels of rainfall and rapidly growing plant species, species composition, density of surviving understory vegetation, as well as regrowth determined by growth form, can set the stage for understory recovery from disturbance (Halpern 1988).

This is especially relevant where initial patterns of community change shift as vegetation density increases and light availability declines relatively quickly due to aggressive vegetation growth responses after seemingly catastrophic disturbances. However, such patterns are dependent on the survival of at least some components of the original plant community (including seeds), and in that sense large surviving trees may play a pivotal role in tephra disturbance sites by providing a physical barrier to disturbance and a nucleus of source propagules for understory re-establishment following gap fall succession or canopy re-establishment (Del Moral and Grishin 1999; Schlawin and Zahawi 2008; Cook and Halpern 2018). Nevertheless, some species (such as small shrubs and trees in this study), may disperse rapidly in years following disturbance, and may be adapted to rapid growth in new volcanic substrates independent of large residual trees. For example, Antos and Zobel (1986) found increased density of colonizing conifers (esp. *Tsuga* spp.) in tephra deposits surrounding Mount St. Helens (Wa, USA) in the years immediately following the eruption, and such initial responses were still reflected in the community over 36 years later (Fischer et al. 2019). Dispersal patterns may also be reflected in our results, and many berry-producing shrubs and sub-canopy trees may benefit from bird dispersal where dispersal from dead tree branches (Fig. 1) could result in more seedlings away from tree bases.

The role of large trees in delivering organic material from the canopy concomitant with tephra deposition is an important but understudied factor that contributes to microsite conditions, which may be important to plant growth and survival on newly deposited volcanic substrate. The chemical and physical characteristics of volcanic materials could pose challenges to plant community development in posteruption systems. Volcanic ejecta is typically devoid of important ecosystem soil building blocks, specifically carbon and nitrogen. In the case of the 2015 Calbuco eruption, the specific features of the tephra itself (coarse texture) may have ameliorated this obstacle to plant growth to some degree by abrading existing vegetation, resulting in significant additions of C and N during the eruption. In our data, C, N, and OM adjacent to tree bases were significantly greater than at 3 m from the tree base, while pH was significantly lower. Scoria cover was generally reduced away from canopies, while litter was higher.

It was unclear if the higher C, N, OM, and lower scoria were due to (1) less scoria initially deposited near the base of trees, (2) more mixing of scoria with canopy soil deposits, wood, detritus, and epiphyte mats near the base of trees that were deposited during (or shortly after) the eruption, (3) occasional epiphyte slumping (secondary disturbance) during the three years of measurements, or (4) a combination of these factors. These explanations are not mutually exclusive, and in combination they represent unique mechanisms through which trees may produce 'zones of influence' (sensu Zinke 1962) at the soil surface. Such edaphic differences in microsite are consistent with initial responses of the vegetation community. Additionally, as organic surface material increased through time away from tree bases, we also saw colonizers (e.g., *M. planipes* and *A. luma*) increase with distance from tree bases. However, more controlled substrate response studies will be needed to better understand specific species responses. At our study sites, long-term successional impacts on the forest understory may depend upon the continued survival of the dominant, emergent trees through mechanisms that are not limited to immediate effects on edaphic conditions. If these trees continue to persist and regenerate extensive canopies, light availability will decrease and litter will increase to the forest floor, while substrate for epiphytes will also increase. If large trees eventually succumb due to damages incurred during the eruption, fallen boles will contribute to gap dynamic succession. Additionally, long-term effects of trees on edaphic conditions could include effects on soil microbial communities, soil moisture, and essential micro and macro nutrients.

Regardless, our data suggest that vegetation dynamics near large trees are variable over short distances and can change rapidly in Valdivian rainforests following disturbance by tephra. Our data contribute to the understanding of these forests in that they suggest roles of large trees in vegetation recovery following disturbance by scouring tephra deposits, a disturbance that may be especially common in montane forests of central and southern Chile (Ayris and Delmelle 2012; Swanson et al. 2013; Romero et al. 2016). The patterns we describe through the first three years of measurements may be harbingers of long-term succession trends as have been described in other longitudinal studies (e.g., Antos and Zobel 1986, Fischer et al. 2019). In forest ecosystems that face

frequent and intense disturbances, documenting such complexity early in succession may be important in order to further understand ecological resilience patterns through time.

Authors' contributions LH, DGF, and CMC designed the original study, LH led field data collection in all years with assistance from NF and DGF in select years. DGF conducted all analyses. LH and DGF wrote the original draft. LH, NF, DGF, and CMC contributed text and made significant editorial contributions to the current manuscript draft.

Data availability Data will be made available at OSF.io upon acceptance for publication.

Declarations

Conflict of interest The authors have no conflicts of interest to declare in this work.

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