

Residual Large Trees Influence Short-term Succession Following a Volcanic Eruption in a Valdivian Temperate Rainforest

Lisa Hintz

The Evergreen State College

Dylan Fischer (✉ fischerd@evergreen.edu)

The Evergreen State College <https://orcid.org/0000-0001-5384-9655>

Nina Ferrari

US Forest Service: US Department of Agriculture Forest Service

Charlie M.S. Crisafulli

U.S. Forest Service

Original Research (6,000)

Keywords: Calbuco Volcano, Chile, Patagonia, Tephra, Disturbance ecology, Vegetation

Posted Date: February 5th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-184770/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

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 post-eruption vegetation response include: 1) amelioration of volcanic substrates, 2) as source propagules from the tree or from associated epiphytes, and 3) by sheltering understory vegetation, thereby increasing rate of recovery near tree bases. Here, we evaluate Valdivian temperate rainforest understory vegetation response and soil characteristics 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 tree species. However, significant interactions with year of measurement, and individualistic responses by many species made generalizations more difficult. Small 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 far 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 can modify edaphic conditions and provide important early refugia for vegetative regrowth following a tephra fall event. Nevertheless, complex interactions through time with species and growth form, suggest the influence of large trees on plant establishment and growth with close proximity tree boles is more complex than a simple facilitative model might suggest.

Introduction

Patterns of plant succession following disturbance remain fundamental in ecology (Walker and Wardle 2014; Meiners et al. 2015; Chang et al. 2019). Recovery dynamics, particularly in areas disturbed by volcanic eruptions are not well understood (Cook and Halpern 2018; Chang et al. 2019; Zobel and Antos 2017; Fischer 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 (Ayrís and Delmelle 2012). In the last decade, multiple southern hemisphere volcanic eruptions have resulted in tephra deposition events in temperate rainforests in Chilean Patagonia (Castruccio et al. 2016). Valdivian rainforests of the southern hemisphere have described dynamics in regards to a variety of both small (González et al. 2015) and large (Veblen and Ashton 1978; Kilian et al. 2006) disturbance events (*e.g.*, fire, wind, avalanche, volcanic eruption), but less-so with respect to the impact of tephra deposition on plant succession (Swanson et al. 2016). 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; del Moral 2010; Walker et al. 2013; Magnússon et al. 2014; Crisafulli et al. 2015; Chang et al. 2019).

Tephra effects on ecosystems depend on a variety of abiotic and biotic factors: tephra characteristics (*e.g.*, texture, particle mass, deposit thickness, 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).

A potentially important and understudied influence of post-eruption substrate conditions may be proximity to large trees because large trees can modify microsite conditions. The zone of influence of forest canopies on ecosystems has attracted the attention of researchers for several decades (Veblen and Ashton 1978; Binkley and Giardina 1998), however no study that we are aware of has addressed the role of extant trees (live or dead) in structuring post-tephra deposition plant community development. 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). Additionally, 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 (Callaway 1995; Callaway 2007; Bonanomi et al. 2008) where surviving trees create unique substrate conditions that facilitate other plant species: 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 disproportionately 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 post-eruption 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 safe site for germination and establishment of colonizing species, thereby affecting colonization rates and species composition (Bruno et al. 2003). Similarly, surviving trees may ameliorate post-eruption 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 their role in influencing post-eruption succession of understory and epiphytic species following the 2015 eruption of Calbuco Volcano in the southern Chilean Andes. Specifically, we hypothesize that: 1) residual plant growth would be negatively related to distance from surviving trees in a pattern consistent with the tree zone of influence concept (Zinke 1962) and plant facilitation in harsh environments (Bertness and Callaway 1994), 2) colonization by new seedlings would decline inversely with distance from tree base, 3) patterns would be strongest for bryophyte, epiphytic, and herbaceous species, and would be less-so for shrub and small tree species, 4) percent cover of all species would increase through time, and finally, 5) nutrient and organic matter (OM) levels of the soil adjacent to tree bases would be greater than at non-adjacent sites.

Methods

Study Site

Our research was conducted on the north flank of Calbuco Volcano in the Los Lagos region of southern Chile, 30 km east 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 that is contiguous with Llanquihue National Reserve (33974 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). In the years following the eruption, this area received approximately 2015 mm (2015–2016), 1644 mm (2016–2017), 2282 mm (2017–2018), and 1823 mm (2018–2019) of annual precipitation 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 data available from 2015 – 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 1–2 m canopy radii (Fig. 1). Forests at our study site are dominated by late succession, shade-tolerant *Laureliopsis philippiana* (Atherospermataceae) and *Dasyphyllum diacanthoides* (Asteraceae), with mixed sub-canopy species *Amomyrtus luma* (Myrtaceae) and *Myrceugenia planipes* (Myrtaceae). The dominant shrub species are *Fuchsia magellanica* (Onagraceae), *Ribes magellanicum* (Grossularaceae), *Azara lanceolata* (Salicaceae), 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* (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 as well as several perennial ferns and herbs (hereafter “herbs”) including *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 post-eruption, (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..

Table 1

Taxa (species or species-group) list by growth form with relative dominance (cover) and relative frequency values^a.

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

^aOnly 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.

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 selected using six

10 m x 150 m belt transects arranged roughly along hill-slope contours, predominantly oriented south-to-north.

For each study tree, DBH, geographic location, and elevation were recorded (point-averaged locations based on > 100 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. Sampling transects of 3 m originated from the base of each tree in the direction of the azimuth. Transect length was determined in the field based on remnant canopy radii. 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 or within 1 m of another tree < 65 to ≥ 30 cm DBH. 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 x 40 cm quadrat frame was used to record cover along sampling transects at near the base of the tree (0 and 20 cm), at intermediate distances (50, 90, and 150 cm), and more distant (200, and 270 cm; hereafter “far”) from the base of the tree. Visual cover estimates (cm²) 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 ≥ 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 post-eruption) based on detection of cotyledons, juvenile leaf morphology, or, in some rare cases, careful non-destructive 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 cm² and 100 cm² placards as reference guides to ensure uniformity.

Vegetation was classified into growth form for analysis based on the dominant form and habitat observed at the site. We grouped vegetation into the following growth form categories: Mosses, Liverworts, and Lichens (non-vascular plants and lichens that were found both on tree bases and branches, and on ground surface), Epiphytes (vascular plants primarily found growing on trunks and branches of live trees), 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 cm³ 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. Sub-samples 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 sub-samples of each dried soil sample were combusted for 5 hours at 500 °C in a muffle furnace. Finally, 5–10 mg air-dried sub-samples 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 divided into two steps: 1) analysis by individual species (or taxon), and 2) analysis by growth form. 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 a few plots, and therefore this species was not included in our calculations of relative dominance or frequency.

Data were combined into three distance categories for analysis: “near” (0–20 cm), “intermediate” (50–150 cm), and “far” (200–270 cm) from the base of the tree. Species and growth form data were also centered relative to highest values prior to analysis. To analyze the significance of patterns in % cover with distance from tree base through time, we used a REML mixed model approach. Within each test, differences in cover were evaluated using distance from bole, and year as categorical fixed effects and aspect (direction from tree), forest floor litter cover (inversely correlated with scoria and bare soil cover), 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 non-linear 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), and Satterthwaite’s method was used in the construction of type II ANOVA table to interpret relative significance of fixed effects. 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 cut-off accounting for the number of models tested within each plant growth form in each case where the same dependent variable was used. Post-hoc multiple comparisons following significant models, were conducted using Student’s *t*-tests for multiple comparisons.

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 similarly conducted using a REML approach (distance from bole and year treated as categorical fixed effects and aspect and individual sample location nested within tree ID as random effects) followed by Student’s *t*-tests for multiple comparisons. However, 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 paired *t*-tests comparing adjacent and 3 m distances from each tree. As above, analyses were conducted using R, and an α value of 0.05 was used to denote significance.

Results

Mosses, Lichens, and Liverworts

Consistent with our first hypothesis, moss declined steeply with distance from tree bases in all years (Table 2, Fig. 2). Moss abundance also varied slightly from year to year, and an interaction between year and distance suggested a stronger effect of distance in 2018. On average, moss cover was less than 5% of ground cover at intermediate and far distances from the tree base. Liverwort responses were variable, and there was no consistent pattern with distance from tree bases among years by 2019 (Fig. 2). In contrast, lichen cover increased significantly with distance from the base of trees in 2017 and 2018, but not in 2019 (Table 2, Fig. 2).

Table 2

Type II ANOVA table from REML model for moss, liverworts, and lichen across three years post-eruption near tree bases, intermediate distances from trees, and far from tree bases.

	Source	SS	df	F	P	Significance
Moss	Year	0.136	2, 835.27	16.01	0.000	*
	Distance	0.319	2, 114.79	37.59	0.000	*
	Year x Distance	0.094	4, 834.15	5.55	0.000	*
Liverworts	Year	0.003	2, 848.00	1.85	0.158	
	Distance	0.002	2, 366.71	1.23	0.294	
	Year x Distance	0.007	4, 848.00	2.23	0.064	
Lichen	Year	0.015	2, 791.41	3.82	0.022	
	Distance	0.032	2, 122.09	8.10	0.000	*
	Year x Distance	0.026	4, 848.48	3.26	0.011	*

*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.

Canopy Epiphytes

Consistent with our first 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 (Table 3, Fig. 3). Patterns for third species, *Mitraria coccinea*, were not significantly explained by distance, even while *M. coccinea* in our plots demonstrated a similar general pattern of decline with distance from the base of trees. Residual *Asplenium dareoides* showed no statistically significant change with distance in most years even though samples from our plots indicated and average decline with distance from the base of trees in 2018 (Fig. 3). Colonizing *L. radicans* also demonstrated a statistically significant, yet very small, decline with distance from the base of trees (Table 3), but there were no other statistically significant patterns in individual epiphyte species responses to distance or year of sampling.

Table 3

Type II ANOVA table from REML model for epiphyte species across three years post-eruption near tree bases, intermediate distances from trees, and far from tree bases (2-2.7 m; canopy interspace).

RESIDUALS						
	Source	ss	df	F	P	Significance
<i>Luzuriaga radicans</i>	Year	0.0062	2, 847.94	1.56	0.210	
	Distance	0.0788	2, 103.08	19.79	0.000	*
	Year x Distance	0.0121	4, 847.94	1.52	0.195	
<i>Mitraria coccinea</i>	Year	0.0003	2, 848.01	0.07	0.930	
	Distance	0.0071	2, 122	2.06	0.132	
	Year x Distance	0.0034	4, 848.01	0.48	0.748	
<i>Hydrangea serratifolia</i>	Year	0.0108	2, 847.9	2.01	0.134	
	Distance	0.0834	2, 107.49	15.60	0.000	*
	Year x Distance	0.0145	4, 848.02	1.36	0.247	
COLONIZERS						
	Source	ss	df	F	P	Significance
<i>Luzuriaga radicans</i>	Year	0.0001	2, 1032.8	1.28	0.279	
	Distance	0.0004	2, 1028.2	5.31	0.005	*
	Year x Distance	0.0002	4, 1017.4	1.04	0.385	
<i>Asplenium dareoides</i>	Year	0.0053	2, 787.49	3.16	0.043	
	Distance	0.0012	2, 368.05	0.74	0.480	
	Year x Distance	0.0016	4, 846.83	0.49	0.743	
*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.						

Shrubs and Small Trees

Shrub and small tree relationships with distance from the tree base were variable. Inconsistent with hypothesis one, cover of residual *Chusquea* spp., a shrubby bamboo species, was not significantly different with distance from the tree base or by year. Similarly, vegetative cover of the tree species *Dasyphyllum diacanthoides* did not vary significantly by distance or year. One residual dominant shrub species (*Fuchsia magellanica*) demonstrated significantly higher cover near tree bases regardless of year (Table 4, Fig. 4). Another shrub, *Ribes magellanicum*, demonstrated a significant decrease through time in cover of residual plants, but the apparent 2017 decline in cover with distance from the base of the tree (Fig. 4) was not statistically significant. Finally, the residual occasionally-vining shrub *Solanum valdiviense* was relatively abundant early-on in plots near the bases of trees (Fig. 4), yet patterns with distance and year of measurement were not significant (Table 4).

Table 4

Type II ANOVA table from REML model for residual and colonizing tree and shrub species across three years post-eruption.

RESIDUALS						
	Source	ss	df	F	P	Significance
<i>Amomyrtus luma</i>	Year	0.007	2, 848	1.29	0.275	
	Distance	0.01	2, 209.83	1.81	0.166	
	Year x Distance	0.007	4, 848	0.67	0.609	
<i>Chusquea spp.</i>	Year	0.009	2, 809.28	1.92	0.147	
	Distance	0.003	2, 365.63	0.57	0.564	
	Year x Distance	0.016	4, 845.61	1.67	0.154	
<i>Dasyphyllum diacanthoides</i>	Year	0.002	2, 760.62	1.43	0.241	
	Distance	0.002	2, 145.84	1.28	0.281	
	Year x Distance	0.002	4, 846.11	0.76	0.553	
<i>Fuchsia magellanica</i>	Year	0.024	2, 811.68	5.81	0.003	*
	Distance	0.026	2, 366.99	6.31	0.002	*
	Year x Distance	0.020	4, 844.43	2.41	0.048	
<i>Myrceugenia planipes</i>	Year	0.005	2, 812.52	1.26	0.283	
	Distance	0.005	2, 129.83	1.19	0.306	
	Year x Distance	0.021	4, 841.58	2.66	0.032	
<i>Ribes magellanicum</i>	Year	0.038	2, 848.03	7.28	0.001	*
	Distance	0.009	2, 180.86	1.68	0.189	
	Year x Distance	0.022	4, 848.03	2.11	0.077	
<i>Solanum valdiviense</i>	Year	0.016	2, 780.54	2.70	0.068	
	Distance	0.008	2, 421.76	1.42	0.242	
	Year x Distance	0.013	4, 841.29	1.05	0.380	
COLONIZERS						
	Source	ss	df	F	P	Significance
<i>Amomyrtus luma</i>	Year	0.575	2, 716.08	73.02	0.000	*
	Distance	0.121	2, 130.64	15.33	0.000	*
	Year x Distance	0.167	4, 846.25	10.61	0.000	*
<i>Myrceugenia planipes</i>	Year	0.091	2, 837.04	35.42	0.000	*
	Distance	0.005	2, 114.12	2.08	0.130	
	Year x Distance	0.011	4, 1065.59	2.19	0.068	
<i>Ribes magellanicum</i>	Year	0.003	2, 1272	1.00	0.368	

*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.

RESIDUALS						
	Distance	0.000	2, 1272	0.08	0.924	
	Year x Distance	0.01	4, 1272	1.307	0.265	
<i>Fuchsia magellanica</i>	Year	0.034	2, 745.42	6.03	0.003	*
	Distance	0.009	2, 135.04	1.57	0.212	
	Year x Distance	0.008	4, 845.33	0.72	0.578	
*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.						

For residual trees *Amomyrtus luma* and *Myrceugenia planipes*, the data did not support declines in abundance with distance, and in fact average values for our samples demonstrated an increase in % cover for residuals of both species at intermediate distances, but this pattern was not significant for the larger population.

Inconsistent with hypothesis two, colonizing *A. luma* (a dominant small tree species), cover increased significantly by 2018, and was significantly higher at intermediate and far distances from tree bases after 2018 (Fig. 4). Another important small tree species, *M. planipes*, demonstrated an increase in cover by colonizing individuals by 2019, but higher average values at intermediate and far distances from trees were not statistically significant (Table 4, Fig. 4). Colonizing *R. magelanicum* was not significantly associated with distance or year. Percent cover of colonizing *F. magellanica* increased after 2017, but this was not significantly associated with proximity to tree bases (Table 4; Fig. 4).

Herbaceous Species

Herbaceous taxa represented a small amount of cover, but exhibited some significant patterns. The most abundant herbaceous taxa, *Blechnum* spp. demonstrated both a decline with distance from the tree base, and an increase in the strength of this pattern through time where *Blechnum* spp. had progressively higher cover values near the base of the tree (~ 1.5% in 2017 to ~ 4% in 2019; a significant distance x year interaction; Table 5). Another residual species, *Hypolepis poeppigii*, showed no significant trends with time or distance from tree (Table 5). Among colonizing herbaceous species, *Blechnum* spp. again showed a significant decline with distance from tree bases and increase in cover (esp. near tree bases) through time (Table 5). *Urtica* spp. showed a significant pattern through time (Table 5), where average cover increased to ~ 0.5% by 2019.

Table 5

Type II ANOVA table from REML model for residual and colonizing herbaceous species across three years post-eruption.

RESIDUALS						
	Source	ss	df	<i>F</i>	<i>P</i>	
<i>Blechnum</i> spp.	Year	0.005	2, 881.6	3.89	0.021	
	Distance	0.008	2, 109.45	5.92	0.004	*
	Year x Distance	0.010	4, 847.76	3.71	0.005	*
<i>Hypolepis poeppigii</i>	Year	0.003	2, 1130.44	2.07	0.127	
	Distance	0.003	2, 160.59	1.68	0.191	
	Year x Distance	0.007	4, 1069.04	1.97	0.097	
COLONIZERS						
	Source	ss	df	<i>F</i>	<i>P</i>	
<i>Blechnum</i> spp.	Year	0.013	1, 632.01	10.76	0.001	*
	Distance	0.013	2, 541.65	5.40	0.005	*
	Year x Distance	0.013	2, 541.65	5.40	0.005	*
<i>Urtica</i> sp.	Year	0.299	2, 1222.62	28.42	< 0.001	*
	Distance	0.003	2, 1214.48	0.28	0.753	
	Year x Distance	0.004	4, 1211.28	0.20	0.936	
*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.						

Plant Growth Form

When taxa were grouped and analyzed by growth form, several clear patterns emerged (Table 6, Fig. 5). Combined lichen and bryophyte cover showed a clear and consistent decline with distance from the tree base in all years driven by changes in moss (as discussed above), and a significant distance by year interaction was a result of stronger patterns in 2018 and 2019 (Fig. 5). Similarly, residual epiphytes declined with distance from tree bases in all years, but differences among years were insignificant (Table 5). There was no significant relationship for colonizing epiphytes with distance or among years. Residual shrubs as a group demonstrated a significant decline in total cover through time. In contrast, colonizing shrub cover increased in 2018 (over 2017 values; Fig. 5) and remained higher in 2019 even though any pattern with distance categories was not significant (Table 6). Residual trees did not vary significantly by distance or year. Colonizing trees, however, significantly increased in 2019, when their cover was significantly greater at locations far from the tree base (Table 6, Fig. 5). Finally, herbaceous cover significantly declined with distance from the tree base for residuals across all years, while for colonizing species a significant increase in cover occurred in 2019, regardless of distance from the tree base (Table 5, 6).

Table 6

Type II ANOVA table from REML model for residual and colonizing growth forms across three years post-eruption.

RESIDUALS						COLONIZERS				
	Source	ss	df	<i>F</i>	<i>P</i>	Source	ss	df	<i>F</i>	<i>P</i>
Bryophytes & Liverworts	Year	0.143	2, 837.38	15.98	0.000*					
	Distance	0.304	2, 114.44	34.00	0.000*				N/A	
	Interaction	0.081	4, 833.45	4.525	0.001*					
Epiphytes	Year	0.001	2, 799.31	0.226	0.798	Year	0.000	2, 1057.7	0.77	0.464
	Distance	0.160	2, 112.29	28.241	0.000*	Distance	0.001	2, 1056.8	3.69	0.025
	Interaction	0.003	4, 844.17	0.257	0.906	Interaction	0.000	4, 1056.2	0.35	0.847
Shrubs	Year	0.042	2, 815.31	5.081	0.006*	Year	0.036	2, 742.14	6.34	0.002*
	Distance	0.025	2, 366.82	3.055	0.048	Distance	0.008	2, 135.04	1.45	0.238
	Interaction	0.023	4, 840.18	1.417	0.226	Interaction	0.010	4, 846.08	0.86	0.488
Trees	Year	0.015	2, 848.14	2.289	0.102	Year	0.134	2, 741.54	39.88	< 0.001*
	Distance	0.013	2, 124.76	1.915	0.152	Distance	0.005	2, 118.29	1.60	0.207
	Interaction	0.032	4, 848.14	2.429	0.046	Interaction	0.030	4, 847.28	4.49	0.001*
Herbaceous	Year	0.003	2, 783.8	0.614	0.542	Year	0.325	2, 1212	28.88	0.000*
	Distance	0.048	2, 109.97	10.357	0.000*	Distance	0.005	2, 1212	0.49	0.614
	Interaction	0.012	4, 847.66	1.278	0.277	Interaction	0.005	4, 1212	0.24	0.917

*Significance indicates a significant P value following a Bonferroni correction for a based on number of similar tests run from the same dataset.

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 ($F_{(2, 424)} = 10.480, P < 0.0001$; Fig. 6). Scoria cover also declined by 1/3 to 1/2 over the course of the three years of measurements ($F_{(2, 848)} = 188.105, P < 0.0001$), and each year was also significantly distinct ($P < 0.0125$). There was no significant distance category by year interaction. Litter cover approximately doubled between 2017 and 2019 across all distances ($F_{(2, 848)} = 168.528, P < 0.0001$), and each year was significantly distinct ($P < 0.0125$). Litter cover was significantly lower near the base of trees regardless of year ($F_{(2, 424)} = 9.345, P = 0.0001$), and there was not a significant distance category by year interaction. Year was a significant effect for cover of wood ($F_{(2, 848)} = 14.953, P < 0.0001$) 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, $P = 0.095$). In contrast, soil cover was higher in all years near the base of trees ($F_{(2, 424)} = 58.598$, $P < 0.0001$), but there was no significant effect of year ($F_{(2, 848)} = 0.534$, $P = 0.587$; Fig. 6). An initial pattern indicated litter cover increased steeply from the base of trees and then leveled off at intermediate distances. Interestingly, 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 0.24 respectively). Residual bryophytes and epiphytes were also negatively correlated with scoria cover ($r = -0.17$ and -0.20 respectively), and litter cover ($r = -0.20$, -0.14 respectively). All other correlations between growth form categories and substrate cover had r values < 0.1 .

Data were consistent with our initial hypothesis five in our one-time analysis (2017), where percentage soil N, C, and OM were markedly higher at the base of trees than at 3 m distance ($P < 0.05$, Fig. 7). In contrast, pH was significantly lower adjacent to tree bases than at 3 m distance (Fig. 7).

Discussion

Our results suggest dynamic influences of large, surviving trees on ecological succession in the years immediately following a volcanic tephra disturbance event. While we initially hypothesized strong trends in growth and colonization with distance from the base of trees (hypothesis one and two), differences in responses among growth forms (hypothesis three), an increase in cover through time (hypothesis four), and differences in soil based on distance from tree (hypothesis five), results were more complex. Rather than demonstrating a pattern of uniform positive (facilitative; Bertness and Callaway 1994) or negative (inhibitive; Connell 1983) effects, in general, surviving trees played changing roles depending on the species and growth form in question and time since the disturbance, while effects were also variable among residual and colonizing (seedling) vegetation. While results for some species may also be consistent with tolerance models of succession (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 somewhat consistent with our third hypothesis, but 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 small trees from the mechanical damage associated with scouring tephra deposition disturbance. However, as time and vegetation recovery progressed, colonization of new individuals seemed to occur without regard to 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.

Large trees play an important role in ecosystem recovery from disturbance (Franklin et al. 2000; Manning et al. 2006; Schlawin and Zahawi 2008; Miao et al. 2013). Studies in other systems 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 Jr 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 non-epiphytic species, and the influence is also variable by plant growth form. However, this compounding temporal influence may also be long-lasting due to radiating effects of influence through 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 (hypothesis four), these increases generally occurred rapidly, and were most apparent in the first and second years of sampling. As such, our data show a more complex model where close proximity to large trees is influential on short-term succession for some species following disturbance, but such effects are intertwined individualistic responses within plant communities.

In Valdivian rainforests, the role of large trees in ecological succession and community composition has been heavily 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 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 succession 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 small shrubs and trees may benefit from bird dispersal where dispersal from dead tree branches (Fig. 1) could result in more seedlings away from tree bases.

Volcanic ejecta is typically devoid of important ecosystem soil building blocks, specifically carbon and nitrogen. The chemical and physical characteristics of volcanic materials could pose challenges to plant community development in post-eruption systems. 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, consistent with hypothesis five, 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. 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. 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 they 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 the patterns of succession surrounding large trees can change rapidly in Valdivian rainforests following disturbance by tephra. Initial protection from scouring volcanic deposits provided by surviving trees may be followed by preferential establishment of woody vegetation independent from the base of the same trees. For some species though, surviving trees may serve as consistent nuclei for re-establishment and vegetation recovery. Over-all, 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 (Ayrís and Delmelle 2012; Swanson et al. 2013; Romero et al. 2016). We show that cryptic moss and epiphyte recovery may be predictably associated with survival of large trees, and survival of residual shrubs in some species (esp. *R. magellanicum* and *F. magellanica*) can be equally dependent on large trees. Interestingly, these patterns occur even though expanding cover of several small tree seedlings and saplings (colonizers and residuals) occurred either independent of distance from large trees, or increasing with distance from large trees. These patterns through the first three years of measurements (less than four years after the eruption), may be harbingers of longer-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, understanding the complex roles of legacy large trees may help land managers further understand ecological resilience patterns through time.

Declarations

Acknowledgements

We are grateful to Bárbara Corrales García, Pablo Saumann Molina, and José Jorquera Muñoz of Parque Volcánico Valle los Ulmos for site access, housing, and local knowledge. Additional thanks to Leif Castren, Eduardo Mattos Aguilera, Magdalena Bustos Hevia, and Jordan Vaughan for help with field work. Thanks also to Mauro E. González of Universidad Austral de Chile for intellectual support. This study was funded, in part, by the United States Department of State Benjamin A. Gilman International Scholarship Program and the United States Forest Service Pacific Northwest Research Station.

Funding: This work was supported by a travel abroad scholarship to LH from the United States Department of State Benjamin A. Gilman International Scholarship Program in 2017, funding in the form of data collection resources and daily site access expenses from the U.S. Forest Service during all three field seasons, and sabbatical funding to DGF in 2019 from The Evergreen State College.

Conflicts of interest/Competing interests: The authors have no conflicts of interest to declare in this work.

Availability of data and material: Data are available upon request to the authors.

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.

Literature Cited

1. Abatzoglou JT, Dobrowski SZ, Parks SA, Hegewisch KC (2018) Terraclimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Sci Data* 5:170191
2. Albornoz FE, Gaxiola A, Seaman BJ, Pugnaire FI, Armesto JJ (2013) Nucleation-driven regeneration promotes post-fire recovery in a Chilean temperate forest. *Plant Ecol* 214:765–776
3. Antos, JA, and Zobel, DB (1986) Seedling establishment in forests affected by tephra from Mount St. Helens. *Am. J. Bot* 73:495-499.
4. Ayrís PM, Delmelle P (2012) The immediate environmental effects of tephra emission. *Bull Volcanol* 74:1905–1936
5. Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48

6. Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
7. Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. In: *Plant-induced soil changes: processes and feedbacks*. Springer, pp 89–106
8. Bonanomi G, Rietkerk M, Dekker SC, Mazzoleni S (2008) Islands of fertility induce co-occurring negative and positive plant-soil feedbacks promoting coexistence. *Plant Ecol* 197:207–218
9. Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
10. Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349
11. Callaway RM (2007) Direct mechanisms for facilitation. In: Callaway RM (ed) *Positive interactions and interdependence in plant communities*. Springer Netherlands, Dordrecht, pp 15–116
12. Castruccio A, Clavero J, Segura A, Samaniego P, Roche O, Le Pennec J-L, Droguett B (2016) Eruptive parameters and dynamics of the April 2015 sub-Plinian eruptions of Calbuco volcano (southern Chile). *Bull Volcanol* 78:1–19
13. Chang CC, Halpern CB, Antos JA, Avolio ML, Biswas A, Cook JE, del Moral R, Fischer DG, Holz A, Pabst RJ (2019) Testing conceptual models of early plant succession across a disturbance gradient. *J Ecol* 107:517–530
14. Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
15. Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
16. Cook JE, Halpern CB (2018) Vegetation changes in blown-down and scorched forests 10–26 years after the eruption of Mount St. Helens, Washington, USA. *Plant Ecol* 219:957–972
17. Crisafulli CM, Swanson FJ, Dale VH (2005) Overview of ecological responses to the eruption of Mount St. Helens: 1980–2005. In: *Ecological responses to the 1980 eruption of Mount St. Helens*. Springer, pp 287–299
18. Crisafulli CM, Swanson FJ, Halvorson JJ, Clarkson BD (2015) Volcano ecology: disturbance characteristics and assembly of biological communities. In: *The encyclopedia of volcanoes*. Elsevier, pp 1265–1284
19. del Moral R (2010) The importance of long-term studies of ecosystem reassembly after the eruption of the Kasatochi Island Volcano. *Arct Antarct Alp Res* 42:335–341
20. Del Moral R, Grishin SY (1999) Volcanic disturbances and ecosystem recovery. In: *Ecosystems of disturbed ground*. Elsevier, pp 137–160
21. Elmquist T, Wall M, Berggren A-L, Blix L, Fritioff Å, Rinman U (2001) Tropical forest reorganization after cyclone and fire disturbance in Samoa: remnant trees as biological legacies. *Conserv Ecol* 5:1–13
22. Fischer DG, Antos JA, Biswas A, Zobel DB (2019) Understorey succession after burial by tephra from Mount St. Helens. *J Ecol* 107:531–544
23. Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1:497–510
24. Franklin JF (1990) Biological legacies: a critical management concept from Mount St. Helens. In: *Trans. North American wildlands natural resource conference*. pp 216–219
25. Franklin JF, Halpern CB (1989) *Influence of biological legacies on succession*. USDA Forest Service, Intermountain Research Station, Washington, DC
26. Franklin JF, Lindenmayer D, MacMahon JA, McKee A, Magnuson J, Perry DA, Waide R, Foster D (2000) Threads of continuity. *Conserv Biol Pract* 1:8–16
27. Gil-Solórzano D, Lara-Cabrera S, Lindig-Cisneros R (2009) Effects of organic matter added to sand deposits of volcanic origin on recruitment of seedlings. *Southwest Nat* 54:439–446
28. González ME, Donoso PJ, Szejner P (2015) Tree-fall gaps and patterns of tree recruitment and growth in Andean old-growth forests in south-central Chile. *Bosque* 36:383–394

29. Griggs RF, Shipley JW, Sayre JD, Hagelbarger PR, Hine JS (1919) Scientific results of the Katmai expeditions of the National Geographic Society. IX. Ohio State University
30. Gutiérrez AG, Aravena JC, Carrasco-Farías NV, Christie DA, Fuentes M, Armesto JJ (2008) Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile. *J Biogeogr* 35:1674–1687
31. Halpern CB (1988) Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69:1703–1715
32. Halvorson JJ, Smith JL, Kennedy AC (2005) Lupine effects on soil development and function during early primary succession at Mount St. Helens. In: *Ecological responses to the 1980 eruption of Mount St. Helens*. Springer, pp 243–254
33. Keeton WS, Franklin JF (2005) Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecol Monogr* 75:103–118
34. Kilian R, Biester H, Behrmann J, Baeza O, Fesq-Martin M, Hohner M, Schimpf D, Friedmann A, Mangini A (2006) Millennium-scale volcanic impact on a superhumid and pristine ecosystem. *Geology* 34:609–612
35. Lindig-Cisneros R, Galindo-Vallejo S, Lara-Cabrera S (2006) Vegetation of tephra deposits 50 years after the end of the eruption of the Parícutin Volcano, Mexico. *Southwest Nat* 51:455–462
36. Magnússon B, Magnússon SH, Ólafsson E, Sigurdsson BD (2014) Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. *Biogeosciences* 11:5521–5537
37. Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–321
38. Meiners SJ, Cadotte MW, Fridley JD, Pickett ST, Walker LR (2015) Is successional research nearing its climax? New approaches for understanding dynamic communities. *Funct Ecol* 29:154–164
39. Miao N, Liu S, Shi Z, Ma J, Wang H (2013) A review of ecological effects of remnant trees in degraded forest ecosystems after severe disturbances. *Shengtai Xuebao-Acta Ecol Sin* 33:3889–3897
40. Miller AE, Sherriff RL, Berg EE (2012) Effects of the Novarupta (1912) eruption on forests of south-central Alaska: clues from the tree-ring record. *Alsk Park Sci* 11:74–77
41. Romero JE, Morgavi D, Arzilli F, Daga R, Caselli A, Reckziegel F, Viramonte J, Díaz-Alvarado J, Polacci M, Burton M, Perugini D (2016) Eruption dynamics of the 22–23 April 2015 Calbuco Volcano (Southern Chile): Analyses of tephra fall deposits. *J Volcanol Geotherm Res* 317:15–29
42. R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
43. Schlawin JR, Zahawi RA (2008) 'Nucleating' succession in recovering neotropical wet forests: the legacy of remnant trees. *J Veg Sci* 19:485–492
44. Swanson FJ, Jones J, Crisafulli C, González ME, Lara A (2016) Puyehue-Cordón Caulle eruption of 2011: tephra fall and initial forest responses in the Chilean Andes. *Bosque* 37:85–96
45. Swanson FJ, Jones JA, Crisafulli CM, Lara A (2013) Effects of volcanic and hydrologic processes on forest vegetation: Chaitén Volcano, Chile. *Andean Geol* 40:359–391
46. Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523
47. UNESCO (2011) Bosques templados lluviosos de los Andes. United Nations Educational, Scientific, and Cultural Organization
48. Veblen TT, Ashton DH (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio* 36:149–167
49. Walker LR, Sikes DS, Degange AR, Jewett SC, Michaelson G, Talbot SL, Talbot SS, Wang B, Williams JC (2013) Biological legacies: direct early ecosystem recovery and food web reorganization after a volcanic eruption in Alaska. *Ecoscience* 20:240–251

50. Walker LR, Wardle DA (2014) Plant succession as an integrator of contrasting ecological time scales. *Trends Ecol Evol* 29:504–510
51. Wunderle Jr JM (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *For Ecol Manag* 99:223–235
52. Zinke PJ (1962) The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130–133
53. Zobel DB, Antos JA (2009) Species properties and recovery from disturbance: forest herbs buried by volcanic tephra. *J Veg Sci* 20:650–662
54. Zobel DB, Antos JA (2017) Community reorganization in forest understories buried by volcanic tephra. *Ecosphere* 8:e02045. doi: 10.1002/ecs2.2045

Figures



Figure 1

Defoliated *Laureliopsis phillipianna* canopy trees with limited horizontal canopy width (often < 3m) 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.

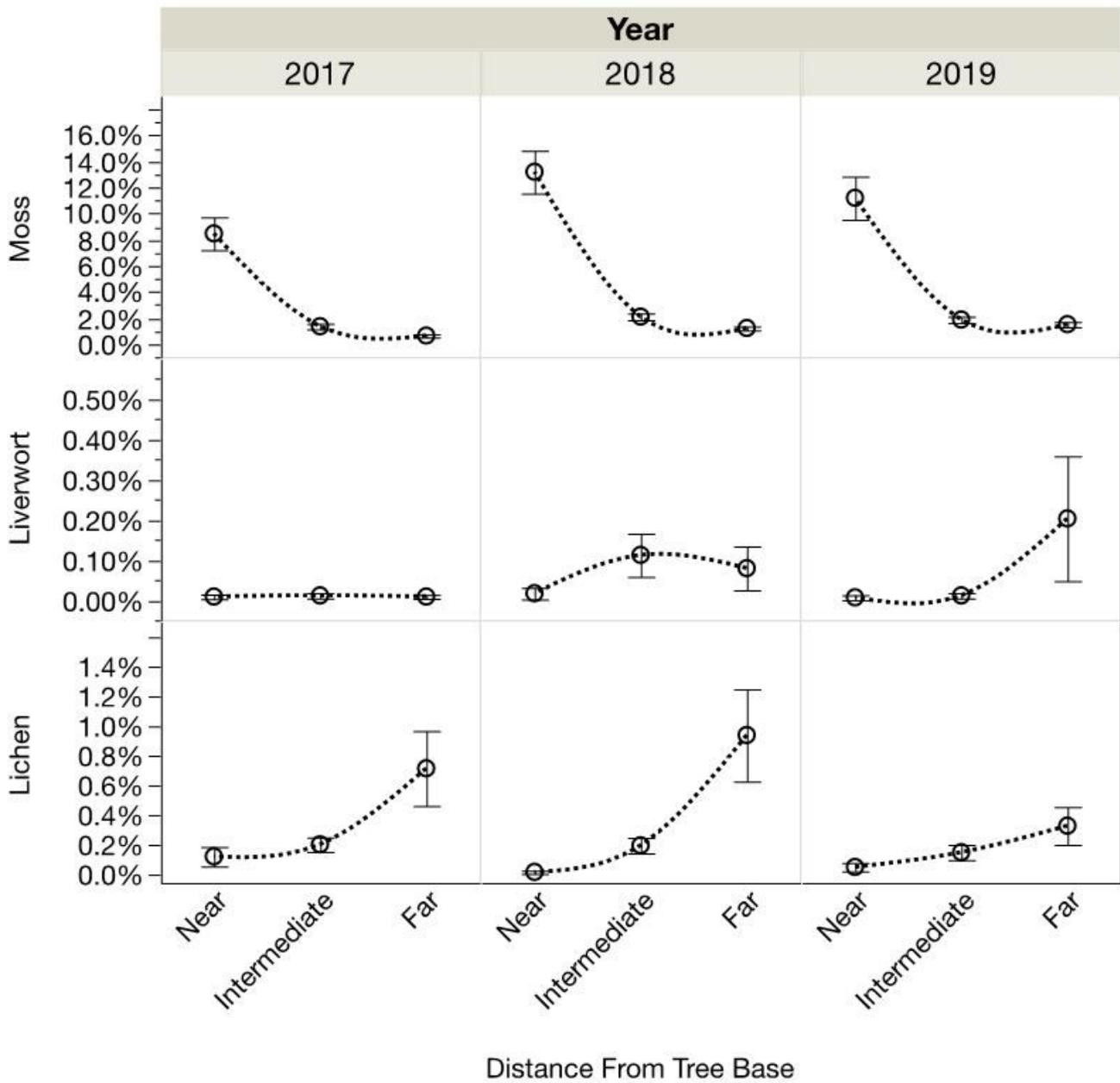


Figure 2

Colonizing moss, liverwort, and lichen cover by distance from tree across all years measured. Points represent means \pm 1 SE.

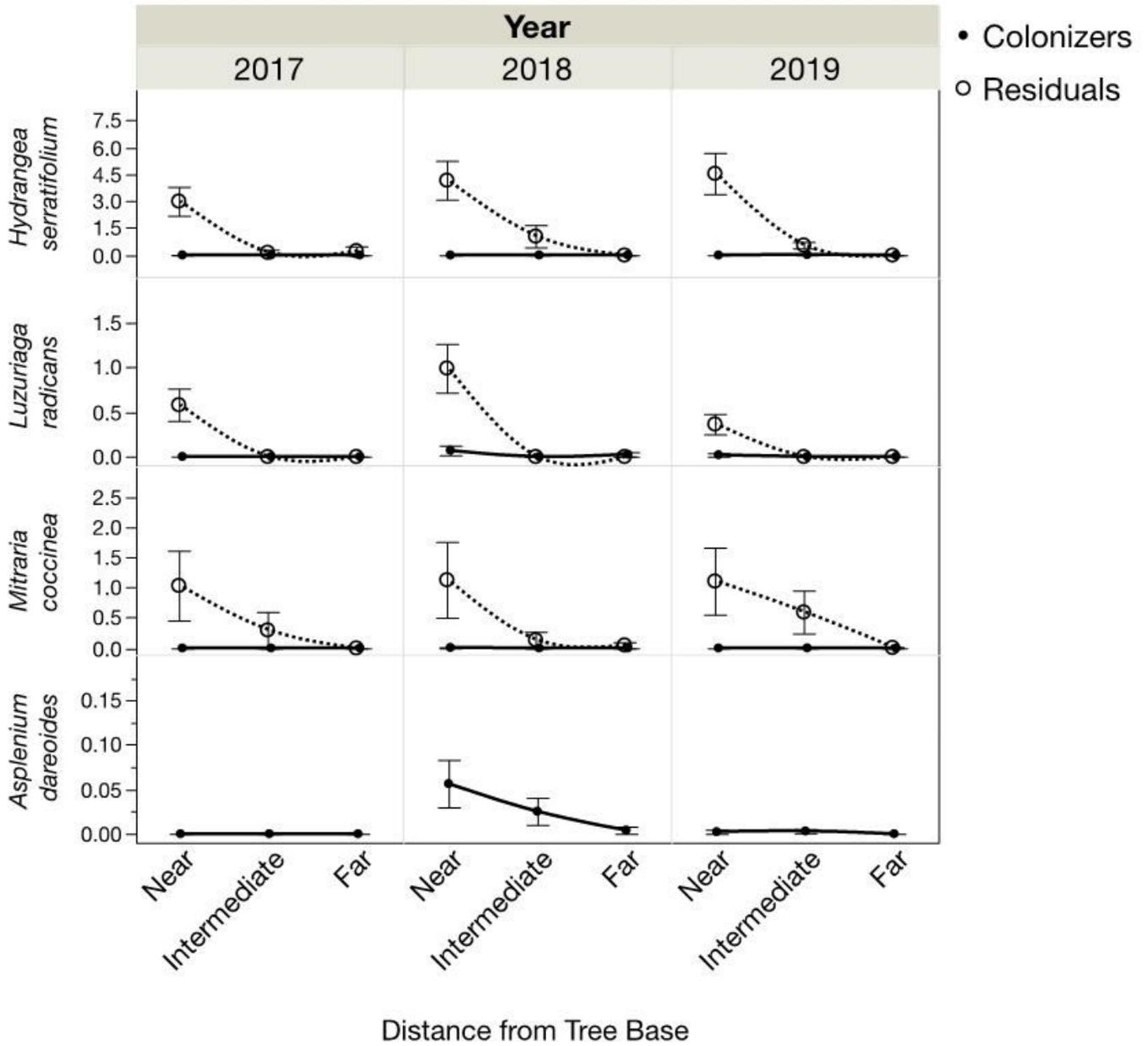


Figure 3

Epiphyte cover by distance from tree across all years measured. Colonizers (filled circles) and residuals (open circles) are plotted separately. Points represent means ± 1 SE.

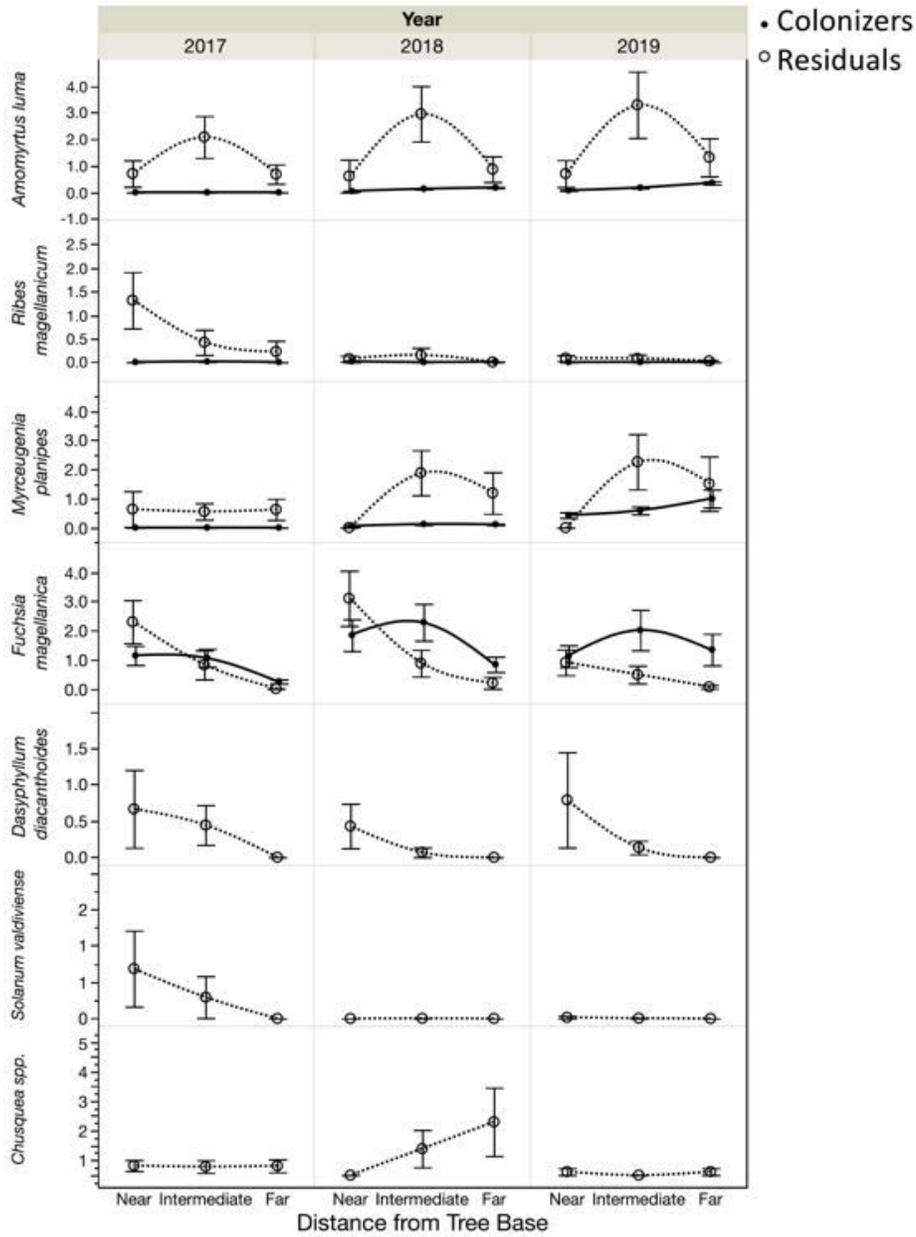


Figure 4

Woody vegetative cover (shrubs and small trees) by distance from tree across all years measured. Colonizers (filled circles) and residuals (open circles) are plotted separately. Points represent means ± 1 SE.

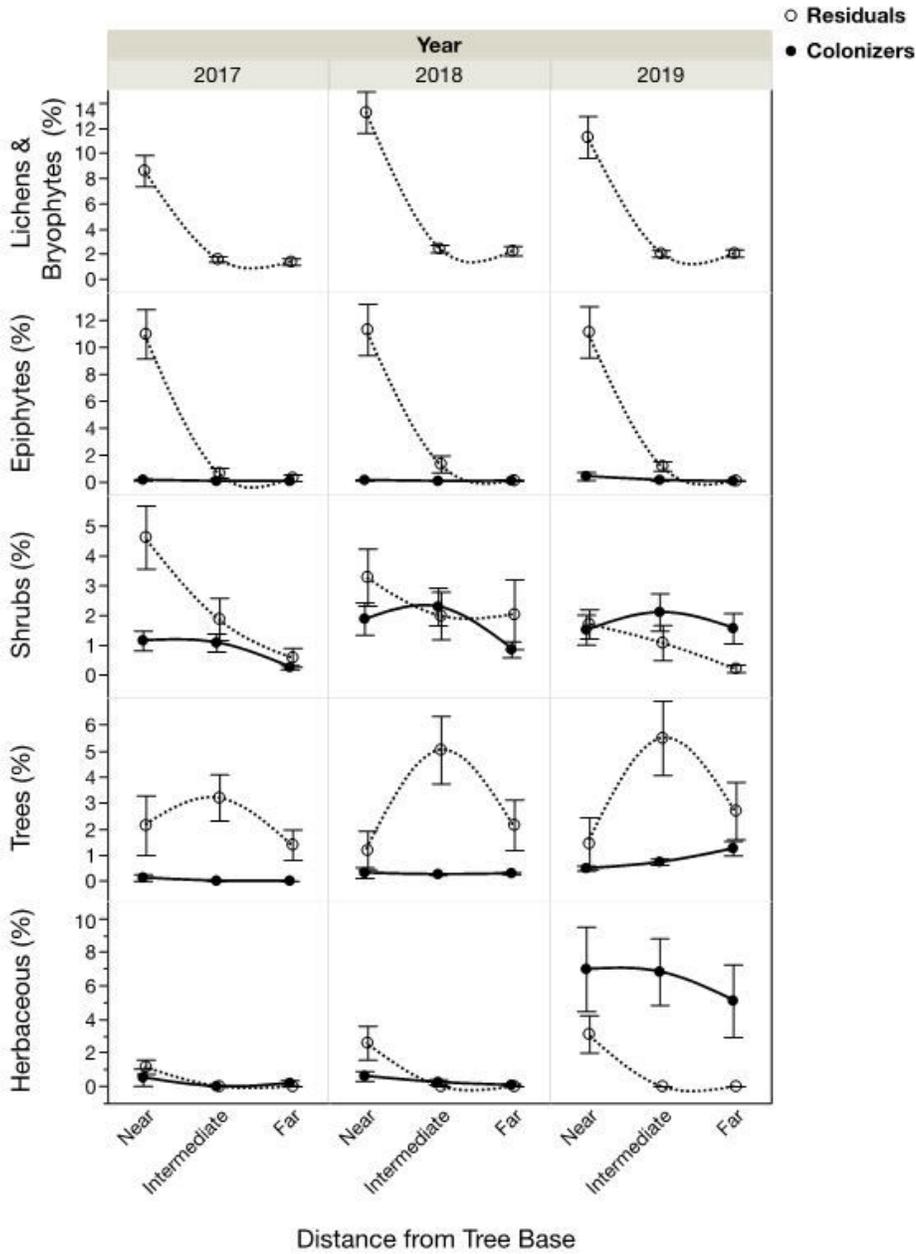


Figure 5

Plant growth form by distance from tree across all years measured. Colonizers (filled circles) and residuals (open circles) are plotted separately. Points represent means \pm 1 SE.

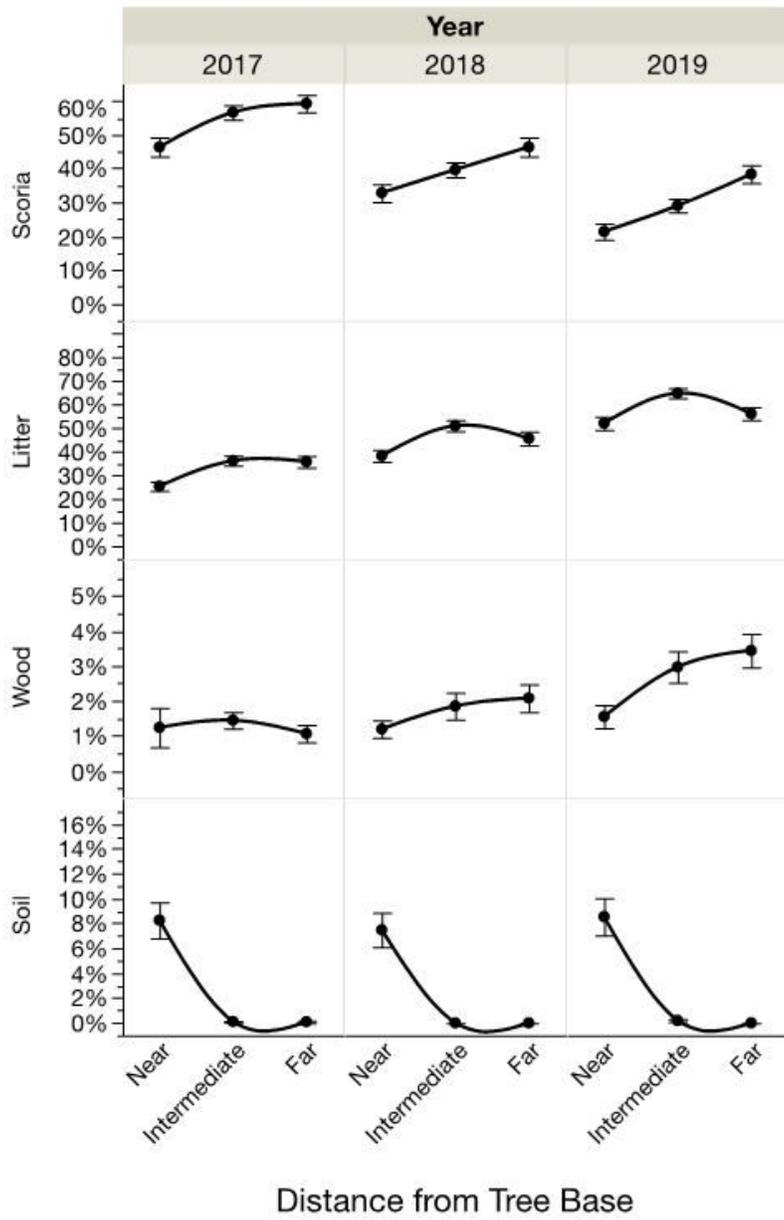


Figure 6

Mean substrate % cover by distance from tree, across all years measured.

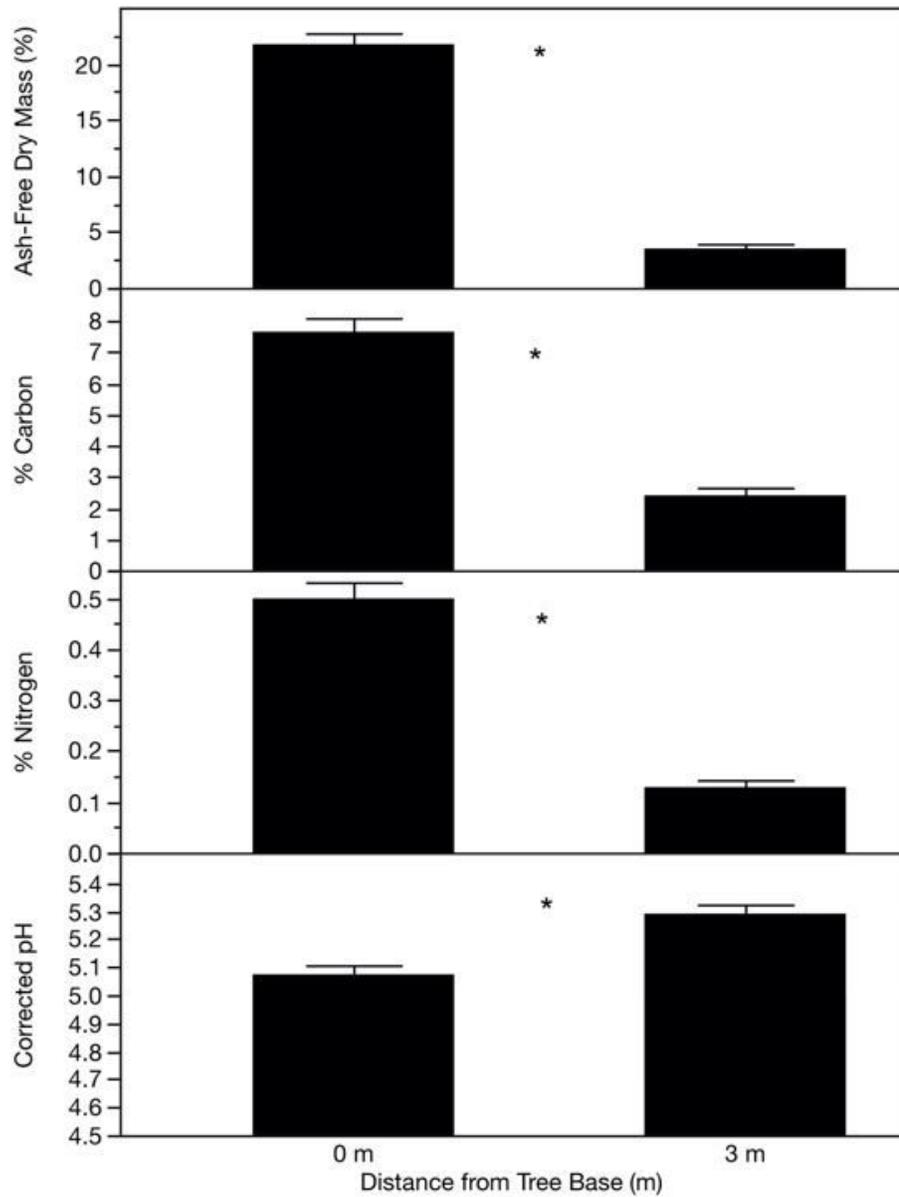


Figure 7

Soil C, N, OM, and pH adjacent to and at 3 m from tree base. Asterisk (*) denotes significant differences at $P < 0.05$. Bars represent means \pm 1 SE.