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RESEARCH ARTICLE

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Topsoil removal through scarification improves natural regeneration in high-graded *Nothofagus* old-growth forests

Daniel P. Soto | **Klaus J. Puettmann**

Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

Correspondence
Daniel P. Soto
Email: dsoto79@gmail.com

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Abstract

1. High grading by removing the majority of trees with superior timber quality has led to loss of productivity and biodiversity in forests. Typically, after high grading, little attention is given to tree regeneration. Thus, undesirable understorey vegetation often dominates for a long time, leading to stagnation in forest recovery and so-called arrested succession. In such settings, managing understorey vegetation using topsoil removal through scarification has been proposed as a restoration tool to encourage tree regeneration.
2. We investigated the effectiveness of topsoil removal as a restoration technique in high-graded *Nothofagus* old-growth forests in the Chilean Andes. In these forests, high grading often leads to understories being dominated by dense thickets of native bamboo, *Chusquea culeou*. These understorey conditions typically delay succession by preventing tree regeneration.
3. *T*-tests were used to compare vegetation development in areas with topsoil removal against those without. Nonparametric multiplicative regression was used to investigate which environmental variables were mainly related to regeneration of different plant groups (short- and long-lived, early- and late-seral tree species) and *C. culeou* abundance in areas with and without topsoil removal.
4. Topsoil removal improved the regeneration of early-seral tree species and constrained *C. culeou*. In areas without topsoil scarification, higher abundances of *C. culeou* were reflected in a higher transmitted radiation and litter cover. In these areas, the presence of early-seral tree species was related to higher soil water content and transmitted radiation. However, topsoil removal altered these response patterns for early-seral trees. For instance, the interaction between higher soil water content and more exposed mineral soil was reflected in a higher likelihood of finding early-seral tree seedlings.
5. *Synthesis and applications*. Topsoil removal was a successful restoration tool for overcoming arrested succession in *Nothofagus* old-growth forests in the Chilean Andes by encouraging the regeneration of early-seral trees in high-graded forests. Contrasting environmental conditions of pre- and post-topsoil removal allowed insights into the processes and mechanisms responsible for forests with arrested succession and for succession progression. This understanding provides guidance regarding the range of conditions under which topsoil removal can be used as a successful restoration practice.

KEYWORDS
arrested succession, bamboo, *Chusquea culeou*, forest regeneration, forest restoration, resilience, understorey vegetation

1 | INTRODUCTION

In many parts of the world, much of the native forest has either been converted to plantations or other land uses and/or has been degraded (FAO, 2010). In the Andean forests in Chile, the large extent of degraded forest is mostly a result of high-grade harvesting (i.e., removal of trees with high timber quality and growth, leaving only trees of poor condition, sensu Lara, Zamorano-Elgueta, Miranda, González, & Reyes, 2016), with little attention paid to tree regeneration (Soto, Donoso, Salas, & Puettmann, 2015). Consequently, regeneration in this temperate region (mostly dominated by *Nothofagus* spp., southern beech) was found to be successful in only about 5% of such high-graded forests (Lara et al., 2016). This can be viewed as a lack of resilience (i.e. "ability of a system or state to absorb disturbance and maintain its functions" sensu Gunderson & Holling, 2002) and appears to be at least partially due to the expansion of native bamboo, *Chusquea culeou* Desvaux. In these conditions (i.e., in 300–800 m^2 canopy gaps after high grading), *C. culeou* often develops into dense thickets that prevent the natural regeneration of *Nothofagus* spp. and other tree species over longer periods of time (González, Veblen, Donoso, & Valeria, 2002; Veblen, 1982). High-graded forests with only damaged and low-vigour trees in the overstorey and with understories dominated by *C. culeou* are viewed as ecologically undesirable in terms of structural and compositional conditions (González et al., 2002; Soto et al., 2015). Specifically, the expansion of *C. culeou* in the understorey is of concern because it negatively affects soil fertility through its deleterious effects of litter on soil nutrients (Veblen, 1982), soil water availability and damage to regenerating trees by mechanical crushing (Griscom & Ashton, 2003). Compared to forests managed according to sustainability principles that encourage high diversity and productivity, conditions after high-grading have negative long-term consequences, both economically and in terms of the provision of other ecosystem services, such as a wide variety of habitat conditions and carbon sequestration (Lu & Buongiorno, 1993).

Concerns about the ecological and economic implications of high grading and the subsequent understories dominated by *C. culeou* have been growing over the last decades, as reflected in increased political discussions and research and restoration efforts (Donoso, Soto, & Fuentes, 2015; Lara et al., 2016). After such overstorey removal, these ecosystems do not follow typical secondary successional patterns, e.g. starting with establishment of early-seral tree species and subsequent build-up of biomass and, in the absence of disturbances, over time a shift in species dominance to late-seral tree species. Instead, the dominance of *C. culeou* results in stagnated vegetation dynamics that can last for 70–120 years (Caccia, Kitzberger, & Chaneton, 2015; González et al., 2002). The environmental and resource conditions after overstorey removal, in conjunction with the expansion and *C. culeou*, a very competitive species, are considered mainly responsible for locking these forests into an arrested succession conditions (Royo & Carson, 2006).

The germination and establishment of early-seral tree species have been shown to be especially sensitive to microsite conditions, e.g., availability of exposed mineral soil or soil water content (Fahey & Puettmann, 2007; Gray & Spies, 1997; Yoshida, Iga, Ozawa, Noguchi, & Shibata, 2005). In contrast, late-seral species are better able to tolerate the low soil water conditions typically found in *Nothofagus* old-growth forests, but only in areas without competition from understorey vegetation (González & Donoso, 1999; Veblen, Schlegel, & Escobar, 1980). In addition, physical barriers, such as thick litter cover, can negatively influence tree establishment in understories, especially of species with small seeds (Christie & Armesto, 2003; González & Donoso, 1999; Sydes & Grime, 1981), such as *Nothofagus* spp. (Donoso, 2006). Thus, ground disturbance (e.g., slash, humus, or topsoil removal by scarification) has been used to manage competitive vegetation and encourage more reliable regeneration of desirable tree species (i.e., mostly early-seral trees) in a number of forest biomes (Löf, Dey, Navarro, & Jacobs, 2012; Örlander, Egnell, & Albrektson, 1996; Reyes, Thiers, & Gerding, 2014; Yoshida et al., 2005).

In this work, we utilized a field study to investigate whether topsoil removal by scarification (hereafter as topsoil removal) is sufficient to push forests out of arrested succession (after partial overstorey removal) by encouraging regeneration of various plant groups, especially early-seral tree species. Furthermore, we documented microsite conditions (small-scale environmental variables, including resource levels) after partial overstorey removal and in areas with and without topsoil removal. The relationships between these conditions and vegetation patterns provide insights which processes may be responsible for potential success of restoration treatments and thus help guide future restoration efforts. We asked the following questions:

1. What environmental conditions are mainly related to the abundance of *C. culeou* (as a species responsible for arrested succession) and to early- and late-seral tree species (as indicators of successional processes) after high grading?
2. Can restoration through topsoil removal overcome arrested succession by reducing undesirable understorey vegetation (*C. culeou*) and encouraging tree regeneration, especially of early-seral species?
3. Does the impact of topsoil removal on environmental conditions and tree abundance provide indications about mechanisms responsible for restoration success?

2 | MATERIALS AND METHODS

2.1 | Study sites

Our study sites (see also Soto et al., 2017) were located between 39° and 40°S latitude and at elevations of 800–1,000 m.a.s.l. in the Andes of south-central Chile, in the Huilo-Huilo biological reserve. Four different sites within the Coihue-Rauli-Tepa forest type in Huilo-Huilo were randomly selected from a pool of sites where the overstorey had been partially removed through high grading and where topsoil removal had been subsequently implemented in portions (a quarter to half) of the high-graded areas (Table 1). We selected sites that had 8 years of understorey response to topsoil removal at the time of sampling. The sites were selected to represent the range of productivity in the region (as reflected in tree height growth; Table 1), were at least 10 ha in size and were on flat or gently sloping ground (<20°). The general characteristics of site and forest conditions are presented in Table 1.

The study conditions were representative of the vegetation zone where *Nothofagus* spp. are most productive. In these types of forests, *Nothofagus dombeyi* and *Nothofagus alpina* were typically the dominant tree species in terms of basal area in the absence of harvesting, with *Saxegothaea conspicua*, *Laureliopsis philippiana* and *Dasyphyllum diacantoides* as minor components found mostly in intermediate and lower canopy layers (Donoso, 2006). Under natural conditions, two major disturbance types influence these forests. First, small-scale disturbances (e.g. individual tree mortality or small canopy gaps of smaller sizes than openings typically found after high-grading) promote intense competition between mid and late-successional trees species, e.g., *S. conspicua*, *L. philippiana* and *D. diacantoides* and bamboo, *Chusquea* spp. (Veblen et al., 1980). Second, less frequent large-scale and intense stand replacing disturbances such as landslides and fire (Pollmann & Veblen, 2004) (openings larger than typically found after high-grading with more soil disturbance) lead to very open conditions. After these disturbances, *N. dombeyi* and *N. alpina* are more competitive because understorey vegetation is mostly removed, and succession follows the model of Bormann and Likens (1979) in terms of biomass build-up and species composition. However, after small- or partial-scale disturbances (e.g. single and multiple treefalls or high-grading; Soto et al., 2015), dense thickets of bamboo species (*Chusquea* spp.) often develop in the understorey, which prevent establishment of shade-intolerant and shade-tolerant tree species for extended periods (González et al., 2002; Veblen, 1982). Bamboo species can dominate a site for 70–120 years until it flowers and dies. Such mortality events create a very narrow window for tree regeneration due to the rapid establishment and growth of *Chusquea* spp. (González et al., 2002; Lusk, 2001; Veblen, 1982).

The climate in Huilo-Huilo is considered Andean polar, with short, dry summers (December–March) and humid winters (June–September). Annual precipitation reaches 3,500 mm (Reyes et al., 2014), mainly as snow during winter. The mean annual temperature is 9°C, with means of 4°C and 16°C for the coldest (August) and warmest (February) months, respectively. Extreme temperatures can range from below −10°C to above 30°C. Thirty to 50 annual frost events are common at 550 m.a.s.l., typically in July and September (Soto et al., 2015).

Soils on the study sites are a transition between Andisol (Acrudoxic Hapludand) and Inceptisol (Andic Dystrudepts). Both are coarse mixed and mesic soils and have a stratified structure and medium texture through the entire profile (Reyes et al., 2014).

TABLE 1 Study site descriptions

Characteristic	Rincón del diablo	Lago chan-chan	Piedras negras	Valle Hermoso
Latitude (°)	39°49′20	39°49′53	39°54′33	40°01′07
Longitude (°)	71°52′27	71°50′34	71°56′50	71°52′32
Altitude (m.a.s.l.)	1,050	1,200	1,030	970
Top-height[a] (m)	41.0 (39.2–44.0)	34.6 (32.4–35.8)	39.0 (37.6–44.5)	44.2 (40.2–48.3)
Density (trees per ha)	145	137	273	285
DBH (cm)[b]	44.0	40.5	34.1	35.4
Basal area (m^2/ha)	50.6	55.8	54.9	63.3
Density of dead trees (trees per ha)	13	25	13	20
Dead tree basal area (m^2/ha)	13.9	19.7	7.5	20.9
Scarified area (%)[c]	45.8	32.5	33.8	24.1
Plots with topsoil removal (%)	42	33	40	28
Slope (%)	0–15	0–20	0–15	0–20
Aspect	SE	SW	E	SE
Soil texture	Sandy loam	Sandy loam	Coarse sands	Loam

[a] Top-height based on 10 largest trees per site.

[b] Mean diameter per site.

[c] Scarified soil was mapped with a resolution of 1 m^2 in all 1-ha permanent plot.

2.2 | Overstorey removal and subsequent understorey response

The overstorey trees on the study sites were partially removed during the summer of 2001/2002 (December–March) by high grading. Even high-grading operations have to follow the Forest Laws established by the Chilean Forest Service-CONAF, i.e., this management practice legally can only remove up to 35% of pre-harvest basal area. On our study sites, this resulted in average residual basal areas of 50–63 m^2/ha and 137–273 trees per ha (measured at the study installation, Table 1) with high patchiness due to the natural variability of tree species, sizes and forms, as well as harvesting and marketing constraints and preferences (Soto et al., 2015). High-graded stands contain few large trees of desirable (*Nothofagus*) spp., few trees with vigorous crowns, and a patchy distribution of residual trees (Soto et al., 2015). After overstorey removal, existing patches of *C. culeou* expanded into dense thickets that covered most of the study sites. In this region, this species reaches 5–6 m in height, an average density of 30–60 culms per m^2, an aboveground biomass of 3,500 g/m^2 (Veblen, 1982). The relatively high average Leaf Area Index of 6 (Lusk, 2001) is also reflected in a dense litter layer on the ground (González & Donoso, 1999). This dense vegetation layer limits diffuse light levels underneath thickets of *C. culeou* to around 1.5%. Examples depicting the residual structure after overstorey removal are shown in Figure S1.

2.3 | Topsoil removal through scarification

Topsoil removal through mechanical scarification was conducted with heavy machinery (Komatzu D4 bulldozer of 5,400 kg, with a horizontal blade) in the summer of 2005–2006. This treatment has the goals of (1) controlling dense tickets of *C. culeou* and remove the dense litter layer, (2) exposing mineral soil as safe sites for germination and establishment of *Nothofagus* spp., and (3) creating open areas for underplanting when seed sources are lacking (Soto et al., 2015). These operations removed the upper soil layers (20–40 cm), including rhizomes and culms of *C. culeou* (Reyes et al., 2014). Topsoil removal created a complex spatial pattern of soil conditions. This disturbance affected portions of all study sites (24%–45% of the study areas, Table 1), i.e., left many small and large openings untreated. The disturbed proportion and spatial distribution varied among sites reflecting the spatial distributions of residuals trees, snags and downed wood (Table 1, Figure 1). In addition, such operations typically avoid removing already existing *Nothofagus* spp. regeneration. This spatial variability, in conjunction with the inherent variability in soils, e.g., due to microtopography, results in a wide range of conditions for tree regeneration. The topsoil removal did not extirpate *C. culeou* from the sites completely, however; in our study sites (Table 1). More information about the effects of topsoil removal through scarification on soil chemical and physical properties on our study sites right after treatments can be found in Reyes et al. (2014).

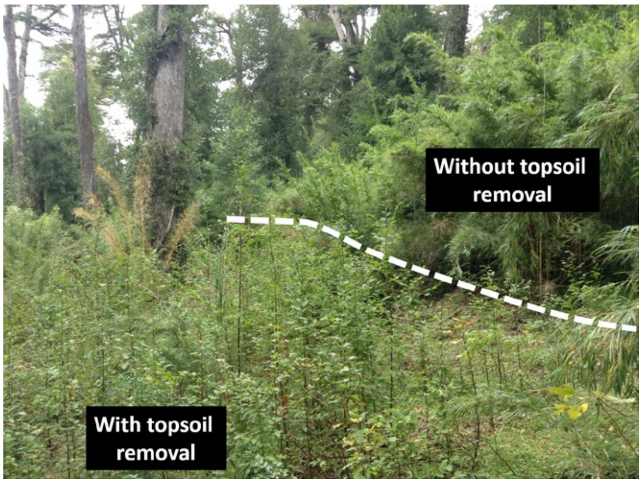

FIGURE 1 Photo depicting the effects of topsoil removal after 8 years in the Valle Hermoso site. Note the clear edge (dashed line) between areas with topsoil removal (to left of line; showing regeneration of SLES and LLES) and areas without topsoil removal (to right of line; showing dense thicket of *Chusquea culeou*). SLES, short-lived early-seral plants; LLES, long-lived early-seral tree species [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Measurements

2.4.1 | Trees and seedlings

Eight years after topsoil removal (i.e., December 2014–March 2015), one permanent square plot of 1 ha (plus a buffer of 10 m on each side) was located randomly in each of the four sites. A 10- by 10-m grid was laid over the 1-ha plots, and centres of regeneration plots of 2 m^2 (radius of 0.8 m) were positioned on all grid intersections (121 regeneration plots in all permanent plots). Regeneration plots were classified based on their location in areas with or without topsoil removal, which after 8 years were still clearly identifiable in field (Figure 1). In the regeneration plots, the percentage of *C. culeou* cover was assessed using ocular estimation (% of cover, accuracy *c.* 5%). The regeneration (seedlings: 5–130 cm in height) was documented using presence (0 = not present, 1 = present) for each of the study species.

2.4.2 | Environmental conditions

We measured the following variables in the regeneration plots: exposed mineral soil (%); litter cover (%); coarse woody debris (woody debris above 10 cm in diameter, %); microtopography (flat, convex, concave and mixed); soil resistance to penetration (kPa); soil volumetric water content and total transmitted radiation (% total light). Soil resistance to penetration was considered an integrated measure of soil disturbance (Soto et al., 2015). We used a cone Fieldscout SC 900 Soil Compaction Meter (Spectrum Instruments, Inc.) with a resolution of 35 kPa and an accuracy of ±103 kPa. Resistance to penetration was measured in five random spots in each regeneration plot. Soil volumetric water content was measured in five random spots in all regeneration plots with a time-domain reflectometer (TDR 100 Soil

Moisture Meter; Field Scout TM; Spectrum Technologies, Inc.), using peer rods of 20 cm. At the centre of regeneration plots, we took hemispherical photographs at 1.5 m above-ground. Light availability was estimated from these photos as total transmitted radiation (a combination of diffuse and direct radiation). For more details about soil resistance to penetration sampling, soil water content sampling and light measurements and calculations, see Appendix S1.

2.5 | Data management

Chusquea culeou abundance (cover, %) were log transformed to improve data normality (0% cover values were replaced by the smallest non-zero value: 1%). Plant species (presence and absence) were divided into three categories based on life span, shade tolerance, maximum height, crown characteristics, rooting patterns and seed size and dispersal (Donoso, 2006):

1. SLES—short-lived early-seral plants (*Ribes* spp. and *Fuchsia* spp.), life span *c.* 30–50 years, small maximum height (<3 m), small, flat root system and fleshy fruits dispersed by birds and small mammals.
2. LLES—long-lived early-seral tree species (*N. dombeyi*, *N. alpina*, *Nothofagus pumilio*), life span >500 years, shade-intolerant, tall maximum height, small crown depths, flat and shallow root system and small, wind-dispersed seeds.
3. LLLS—long-lived late-seral tree species (*L. philippiana* and *Dasyphyllum diacantaoides*), life span >500 years, shade-tolerant, intermediate maximum height, large tree crowns, deep root system and wind-dispersed seed.

2.6 | Statistical analysis

2.6.1 | General overview

First, we tested data normality for species responses individually, using the Shapiro–Wilk test, and we assessed homoscedasticity with Levene's tests (Dytham, 2003). To assess the effectiveness of topsoil removal, we performed paired *t*-tests for abundance of *C. culeou* and plot counts of SLES, LLES and LLLS regeneration separately. All tests used an $\alpha \leq 0.05$.

2.6.2 | Species group–habitat relationships

We used nonparametric multiplicative regression (NPMR) in HyperNiche (McCune & Mefford, 2009) to quantify the relationships between plant groups (abundance of *C. culeou* and presence of SLES, LLES and LLLS) and environmental predictors (McCune, 2006). NPMR avoids distributional assumptions, can accommodate a wide range of response surface shapes, unbalanced data, and uses a free search of the best predictor combination (McCune, 2006). We used the Gaussian weighting kernel and local mean estimator (LM-NPMR; for further details, see McCune, 2006). The predictor variables used to address questions 1 and 2 included exposed mineral soil, litter cover, coarse woody debris, microtopography, soil resistance to penetration, soil water content and transmitted radiation.

Evaluation procedures in NPMR differ for continuous (abundance) and binary (presence/absence) data. Thus, the model was optimized for the abundance of *C. culeou* cover (continuous data) by minimizing minimum average neighbourhood sizes (i.e., N^*, see McCune, 2006). Standard deviations (tolerance) of the kernel functions were optimized by improving the cross-validated coefficient of determination R^2 (xR^2). xR^2 has the same interpretation as the classical R^2, but its calculation differs from R^2 because it is penalized by leave-one-out cross-validation and thus controls for overfitting (see McCune, 2006).

For assessing occurrences (presence/absence, i.e., binary response variables), NPMR uses the Bayes factor to evaluate model quality, comparing a candidate model (M_1) against a "naive model" (M_2) to determine which provides a higher probability of correctly predicting occurrences of groups (McCune, 2006). For model comparisons, this approach uses the log-likelihood ratio to compare the presence or absence of seral groups in a given plot, using the same probability of the two tested models: i.e., $P(M_1) = P(M_2) = 0.5$. Thus, the ratio likelihood B_{12} from observed occurrences ($\mathbf{y} = y_1, y_2, \ldots, y_i$) against the likelihood of the M_2 model is calculated as follows:

$$B_{12} = \frac{P(\mathbf{y}|M_1)}{P(\mathbf{y}|M_2)} \quad (1)$$

where,

$$P(\mathbf{y}|M_j) = \Pi_{i=1}^{n} \hat{y}_i^{y_i}(1-\hat{y}_i)^{1-y_i} \quad (2)$$

$\hat{y}_i$ is the fitted and y_i is the observed values for the likelihood from the *i*th occurrence data for each model, M_j, $j = M_1, M_2$. Equation 2 is the joint probability function of *n* observations of y_i, where each observation is an ordinary Bernoulli random variable (McCune, 2006). For a better interpretation of Bayes Factor values, we used log (B_{12}), where log B_{12} values of 0–0.5 indicate minor, 0.5–1 substantial, 1–2 strong and >2 decisive support (McCune & Mefford, 2009). Because of the nonparametric nature of this approach, we conducted sensitivity analyses in Hyper Niche to evaluate the relative contribution of predictors for candidate models (McCune & Mefford, 2009).

3 | RESULTS

3.1 | General trends

Topsoil removal was successful in reducing the abundance of *C. culeou* from an average of 36% of cover in areas without topsoil removal to 5% cover in areas with topsoil removal and at the same time encouraged regeneration of early successional species (Figure 1, Table 2). Topsoil removal also lead to areas without any *C. culeou*; the number of plots with *C. culeou* cover was significantly lower in areas with topsoil removal compared to areas without topsoil removal ($p < .001$, Table 2). In contrast, SLES and LLES were found in significantly more

TABLE 2 Average number of plots (standard deviation) in which at least one plant of SLES, LLES and LLLS found in plots without and with topsoil removal. The bottom row presents abundance of *Chusquea culeou* (% cover) per soil conditions (without and with topsoil removal). *p*-values indicate the results of paired *t*-tests comparing occurrence in plots with and without ground disturbance for each species group

Species group	Without topsoil removal	With topsoil removal	*p*-value
SLES	13.5 (7.9)	28.5 (9.9)	*
LLES	10.5 (6.4)	31.7 (11.5)	*
LLLS	14.7 (22.7)	8.7 (10.8)	ns
Chusquea culeou	49.0 (14.1)	8.0 (5.2)	**

ns, not significant; SLES, short-lived early-seral plants; LLES, long-lived early-seral tree species; LLLS, long-lived late-seral tree species.
$^*p < .05$, $^{**}p < .01$.

plots in areas with disturbed soils than in areas with undisturbed soils ($p < .05$). The occurrence of LLLS species did not appear to be influenced by this ground disturbance ($p > .05$).

3.2 | *Chusquea culeou* responses to environmental conditions in undisturbed and disturbed soils

The abundance of *C. culeou* showed similar (but not equivalent) patterns in soils with and without topsoil removal. It was significantly positively correlated to transmitted radiation and litter cover in areas without topsoil removal (Figure 2). The cross-validated R^2 for the prediction of abundance of *C. culeou* cover (xR^2 = 23.5%, $p < .001$) in undisturbed soils and was higher when information from both predictors transmitted radiation and litter cover were incorporated into the model (Table 3), suggesting that the interaction between these two variables is a major influence on *C. culeou* dominance in undisturbed soils (Figure 2). However, the sensitivity analyses showed that in undisturbed ground conditions, the amount of transmitted radiation was more influential on *C. culeou* cover than was litter cover (Table 3). In contrast, for topsoil removal conditions, the NPMR model for the abundance of *C. culeou* was not significant (xR^2 = 6.4%, $p > .05$). Even with the low variance explained by these models, transmitted radiation had a higher influence on *C. culeou* than litter cover (Table 3) in areas with topsoil removal.

3.3 | Plant groups' responses to environmental conditions in soils with and without topsoil removal

In areas with topsoil removal, soil water content was the main driver for the presence of all plant groups (except *C. culeou*), followed by transmitted radiation (Figure 3a,c,e). All models with both predictor variables showed a better fit in predicting occurrences of SLES, LLES and LLLS species groups (Table 3). The model predicting the probability of finding LLES species had decisive support ($\log B_{12}$ = 2.9; for interpretation of values, see section“2.6”) and the model for SLES species had strong statistical support ($\log B_{12}$ = 1.7) (Table 3). Sensitivity analyses and low tolerance (*SD*) suggested that soil water content was a more influential (positive) predictor variable for these two early-seral species groups than was transmitted radiation (positive) (Table 3). Similarly, the model predicting the likelihood of finding a seedling of the late-seral species group had decisive statistical support ($\log B_{12}$ = 4.6), and predictions improved when soil water content and transmitted radiation variables were used (Table 3). In contrast to the SLES and LLES species groups, however, low soil water content and higher transmitted radiation were related to a higher probability of finding a seedling of the LLLS species plant group (Figure 3e). Just as for the early species groups, the sensitivity analysis showed that soil water content was more influential than transmitted radiation for late-seral species (Table 3).

The predictive ability of NPMR-estimated models for all seral species groups was higher in areas with topsoil removal (Figure 3b,d,f). However, different environmental conditions were responsible for the occurrence of early-seral species (Table 3). For example, influential predictor variables for SLES occurrence ($\log B_{12}$ = 2.7) included transmitted radiation (positive) and to a lesser extent exposed mineral soil (positive). In contrast, LLES occurrence ($\log B_{12}$ = 4.3) was mostly influenced by soil water content (positive) and to a lesser extent by exposed mineral soil (positive) (Figure 3). Finally, the model for predicting LLLS occurrence had decisive statistical support ($\log B_{12}$ = 5.6). Similar to the relationships in undisturbed soil conditions, low soil water content and higher transmitted radiation increased the probability of finding seedlings of this group (Figure 3f).

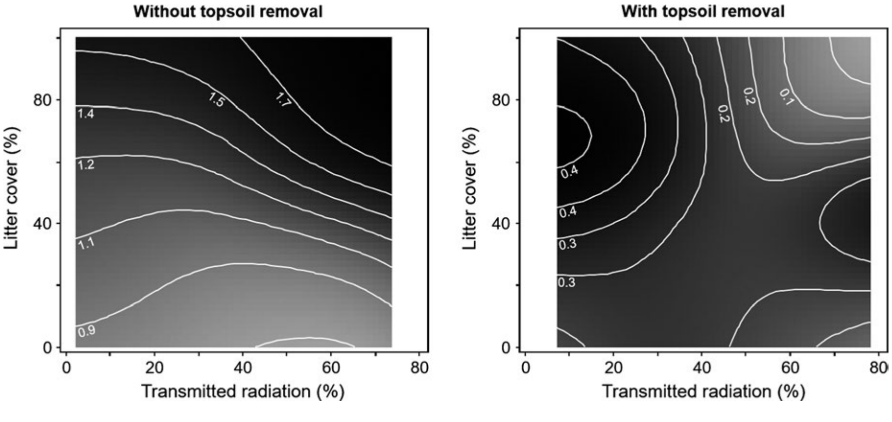

FIGURE 2 NPMR-LM contour plots showing abundance of *Chusquea culeou* (log % of cover) as a function of the best supported predictors for areas with and without topsoil removal through scarification. Darker areas indicate higher abundance. NPMR-LM, nonparametric multiplicative regression-local mean

TABLE 3 Best-fitted nonparametric multiplicative regression models (rows) for prediction of abundance of *Chusquea culeou* (log %). xR^2 is the cross-validated coefficient of determination, $\log B_{12}$ is the Bayes factor coefficient and N^* is the neighbourhood size in the fitting. Tolerance values are for the best predictors (in parentheses) in the free searching procedure using Hypeniche (McCune & Mefford, 2009)

Ground conditions	Species group	xR^2	N^*	Tolerance 1	Tolerance 2
Without topsoil removal	*Chusquea culeou*	0.235	25.7	14.3 (light)	20.0 (litter cover)
With topsoil removal	*Chusquea culeou*	0.064ns	22.1	14.1 (light)	20.0 (litter cover)
Ground conditions	Species group	$\log B_{12}$	N^*	Tolerance 1	Tolerance 2
Without topsoil removal	SLES	1.7	31.9	8.3 (SWC)	14.3 (light)
	LLES	2.9	45.5	8.3 (SWC)	14.2 (light)
	LLLS	4.6	43.6	8.3 (SWC)	28.5 (light)
With topsoil removal	SLES	2.7	65.9	14.1 (light)	38.0 (SM)
	LLES	4.3	10.5	8.4 (SWC)	38.0 (SM)
	LLLS	5.6	13.5	8.3 (SWC)	16.0 (light)

light, transmitted radiation; SWC, soil water content; SM, exposed mineral soil; SLES, short-lived early-seral plants; LLES, long-lived early-seral tree species; LLLS, long-lived late-seral tree species.
ns, no significant, $^*p < 0.001$.

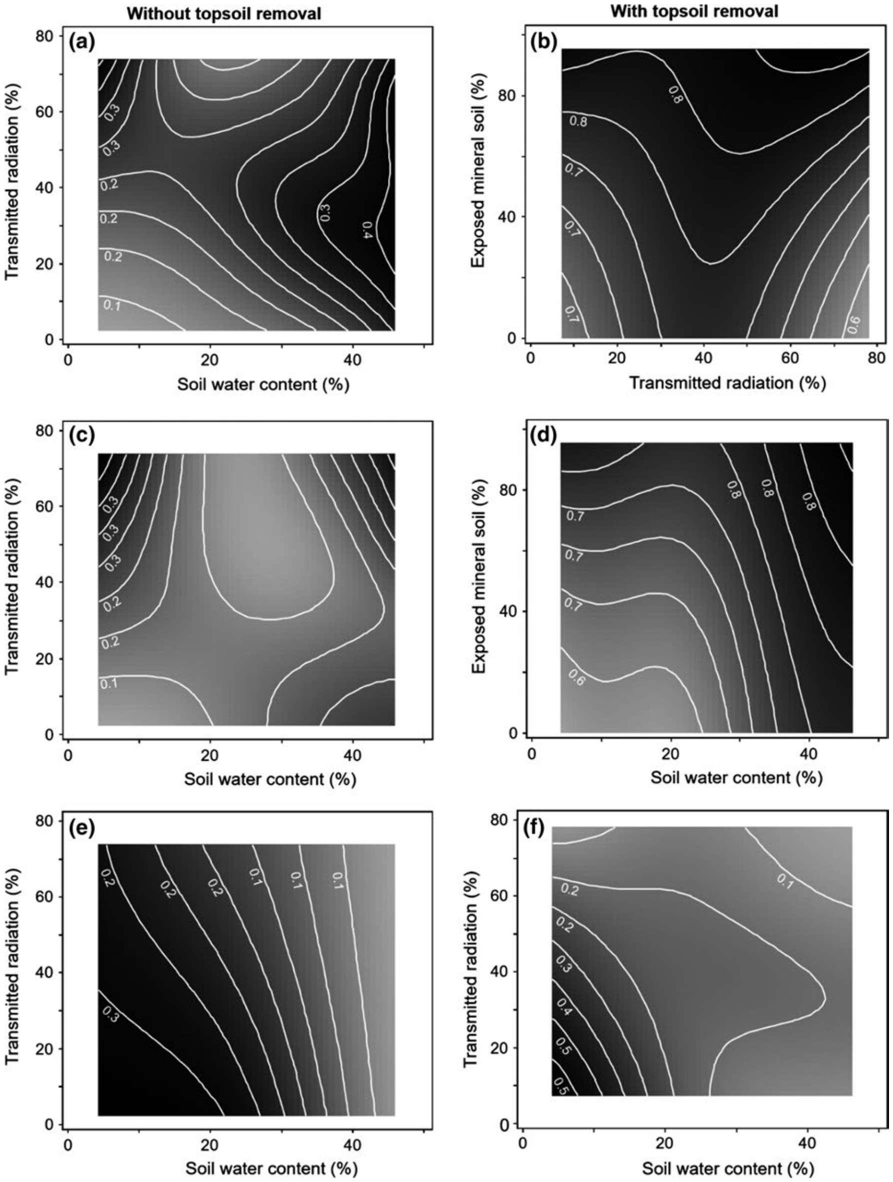

FIGURE 3 NPMR-LM contour plots showing the probability of seedling presence as a function of the best supported predictors for areas with and without topsoil removal through scarification. (a, b) Results for SLES, (c, d) for LLES, and (e, f) for LLLS. Darker areas indicate areas with higher probability of seedlings. SLES, short-lived early-seral plants; LLES, long-lived early-seral tree species; LLLS, long-lived late-seral tree species

4 | DISCUSSION

Our study showed that topsoil removal was a successful treatment in high-graded *Nothofagus* forests in the Andes of south-central Chile, as it reduced the abundance of *C. culeou* and at the same time encourages the regeneration of desirable LLES tree species. This supports findings in a number of forest biomes that this ground disturbance can be an effective practice for altering understorey vegetation to encourage tree regeneration (Löf et al., 2012; Örlander et al., 1996; Reyes et al., 2014; Yoshida et al., 2005). Research has shown that a variety of environmental conditions can be responsible for this effect, including the amount of soil exposure needed to provide safe sites (Cornett, Reich, Puettmann, & Frelich, 2000), degree of soil compaction (Ampoorter, De Frenne, Hermy, & Verheyen, 2010; Soto, Donoso & Puettmann, 2014) and soil fertility (Ampoorter et al., 2010; Reyes et al., 2014). We showed that the relevant factors may not only vary due to environmental conditions, as suggested by the studies above, but also varied for different species groups, likely due to the different traits for each group, such as shade tolerance and seed dispersal patterns (Pywell et al., 2003).

4.1 | Environmental and ecological conditions influencing regeneration plant groups

Given that all study species are frequently found in nearby forests, we assumed that propagules were readily available and that their regeneration dynamics were responding to changes in environmental conditions, as influenced by disturbance (overstorey and topsoil removal) and other plant interactions, such as competition. In this light, our study confirmed that *C. culeou* was dominant—to the detriment of other species, even late-seral species—after partial overstorey removal (high-grading) and before (or without) topsoil removal (González et al., 2002; Veblen, 1982). The expansion of *C. culeou* cover during the first few years after partial overstorey removal (without topsoil removal) has previously been attributed mainly to increases in light availability (González et al., 2002; Veblen, 1982), with less attention paid to other environmental variables (Royo & Carson, 2006). Our results also suggest that the dense cover of leaf litter, low soil water content, and increases in light availability interact to promote the dominance of *C. culeou* in forests without topsoil removal. Thus, this dominance in undisturbed soils was likely facilitated by the fact that early-seral species are not competitive in late-successional understorey settings (Caccia et al., 2015; González et al., 2002). At the same time, the dense *C. culeou* thickets led to high accumulation of litter on the ground, suggesting a positive feedback loop that further reduces the likelihood of tree regeneration (González & Donoso, 1999). Both competition for below-ground resources (soil water and nutrients) and negative impacts on seed germination through litterfall appeared important (Christie & Armesto, 2003; Sydes & Grime, 1981). However, the study setup did not allow us to separate these two processes. Despite this limitation, our results confirmed that a second disturbance that impacts both factors is needed after partial overstorey removal to encourage the early-seral tree regeneration.

In contrast to earlier findings (Pollmann & Veblen, 2004; Soto et al., 2015), our study pointed out that the interaction of exposed mineral and soil water content with light availability is related to the regeneration of early-seral species (LLES and SLES). Light availability in isolation has been commonly assumed to be the major driver for establishment and growth of these species (Pollmann & Veblen, 2004; Veblen et al., 1980). In this study, we found that transmitted radiation did not play such a dominant role in the establishment process. Instead, our results pointed out that the presence of regeneration was related to an interaction of soil water content with transmitted radiation for all species groups in undisturbed soil conditions. In contrast, the interaction of exposed mineral soil (LLES and SLES), soil water content (LLLS) and transmitted radiation was influential in disturbed soils, highlighting the complexity of factors influencing plant regeneration (Schupp, 1995).

Studies have shown the growth plasticity of *N. dombeyi* and *N. alpina*, in terms of light requirements during early stages of regeneration, allowed seedlings to establish and persist under deep shade in areas with relatively little competition from other understorey species (Donoso et al., 2015; Pollmann & Veblen, 2004). Thus, topsoil removal that constrained the abundance of *C. culeou* led to an increase in the regeneration of early-seral *N. dombeyi* and *N. alpina*, likely due to a combination of providing more soil water and exposed mineral soil, and increased light.

4.2 | Partial overstorey removal and ground disturbance in a larger ecological perspective

To properly place our findings on the influence of disturbances (overstorey removal and topsoil removal) and their associated impact on environmental variables into the context of vegetation dynamics, the dynamics themselves must be placed within a larger theoretical perspective, reflecting the importance of cross-scale hierarchies in complex adaptive systems (Messier, Puettmann, & Coates, 2013). As our study pointed out, one of the main drivers of vegetation development was the presence of *C. culeou*, which is a common component (typically found in patchy distributions) in almost all undisturbed, late-successional, temperate old-growth forests in South America (Caccia et al., 2015; González et al., 2002; Veblen, 1982). Partial overstorey removal through high grading appeared to create conditions that were suitable for the expansion of *C. culeou* and consequently unsuitable for the regeneration of early- or late-seral tree species that otherwise would replace the harvested trees to achieve full stocking. Rather than moving relatively quickly through the reorganization phase (sensu Gunderson & Holling, 2002) and following more standard successional development patterns, the environmental conditions in high-graded *Nothofagus* forests are instead suitable for the expansion and dominance of *C. culeou*. Due to the longevity of *C. culeou*, these conditions typically lead to an extended dominance of dense thickets of *C. culeou* within many high-graded old-growth *Nothofagus* forests. Such stagnation in ecosystem development exemplifies a rigidity trap. In such traps, "strong self-reinforcing controls prevent the flexibility needed for the system to adapt" to external changes (Carpenter &

Brock, 2008). The high connectedness (i.e. rigidity of internal control; sensu Gunderson & Holling, 2002) of ecosystems in rigidity traps is evident, when typical small-scale disturbances in these forests, such as a single treefall gap, snow and ice breakage, and animal damage, do not initiate a substantial shift in forest structure and composition. Instead, as long as this internal control is still "rigid," any impacted areas are relatively quickly filled with more *C. culeou*. In these forests, the internal control apparently is overcome by larger or more intensive disturbances, e.g., the topsoil removal and thus removal of a large proportion of *C. culeou*. Only then can standard successional patterns resume (Carpenter & Brock, 2008).

4.3 | Implication for forest restoration

Our study showed that topsoil removal by mechanical scarification can be an effective restoration tool for overcoming arrested succession after high grading in the studied forests. In addition, our findings provide insights into how environmental conditions are influenced by overstorey removal and topsoil removal and, in turn, how these changes in conditions are reflected in vegetation dynamics. Specifically, our study showed that other resources besides light, e.g., soil moisture, may also be influential in driving tree regeneration in the studied forests and restoration treatments should reflect this. Thus, a close examination of soil conditions, specifically nutrient and soil water conditions, will provide insights into the likelihood of success when applying topsoil removal as a restoration treatments. Earlier work (Reyes et al., 2014) also pointed out that soil structure, specifically the potential for soil compaction, needs to be considered when such restoration treatments are applied across a broader landscape.

A basic understanding of these conditions and their interactions and influences is especially helpful when restoration treatments are applied to novel conditions (Hobbs, Higgs, & Harris, 2009), where past experiences are not necessarily helpful or sufficient for a current treatment selection. For example, if climate change leads to more drought events, the prominent influence of soil moisture conditions suggests a higher need for restoration treatments, such as ground disturbance, in order to overcome *C. culeou* dominance in high-graded stands. In addition, viewing plants in terms of traits related to regeneration processes, rather than focusing on life-forms, appears to be useful when selecting restoration treatments (Pywell et al., 2003). Plant traits that are directly linked to resource use or environmental conditions can provide a more mechanistic understanding of vegetation dynamics. Such understanding also facilitates the extrapolation of study findings to other ecosystems (Pywell et al., 2003).

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AUTHORS' CONTRIBUTIONS

D.P.S. designed the study, methodology, performed analysis and was the lead writer. K.J.P. designed the study and edited the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https:/doi.org/10.5061/dryad.3q977 (Soto & Puettmann, 2017).

ORCID

Daniel P. Soto http://orcid.org/0000-0002-7119-8558

Klaus Puettmann http://orcid.org/0000-0002-9736-5924

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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