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Beyond Control: Short-Term Legacy Effects of Invasive Nonnative Trees May Halt Biodiversity Recovery

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ABSTRACT

Questions: Invasive nonnative trees can induce substantial and long-lasting changes in ecosystem structure and environmental conditions. Although numerous management efforts have removed invasive trees, the outcomes have been highly variable, and it remains uncertain whether such interventions are sufficient to restore biodiversity and microclimate. These differences often depend on the invasive species involved and the characteristics of the invaded ecosystem. Here, we evaluate whether the removal of *Pinus contorta* promotes short-term recovery of microclimate and plant diversity in two contrasting Patagonian vegetation types.

Location: Southern Chile, in *Araucaria araucana* forests (−38° S) and Patagonian steppe (−45° S).

Methods: We established paired invaded and removal plots along invasion gradients at both sites. Environmental variables (soil and air temperature, moisture, light, canopy cover, litter) and plant diversity were monitored for 2 years before and after mechanical removal of *P. contorta*. We used linear (LMM) and generalized linear mixed models (GLMM) to test for recovery versus persistent legacy effects.

Results: Removal reduced pine litter and canopy cover, partially restoring microclimatic conditions moderating temperature extremes (i.e., increasing minimum temperatures and lowering maximum temperatures) and increasing soil moisture and light availability. However, native plant richness and abundance showed no signs of recovery, whereas nonnative species significantly increased in the Patagonian steppe.

Conclusions: Our results demonstrate that, despite improvements in physical conditions, legacy effects of *P. contorta* invasion strongly constrain biodiversity recovery in both ecosystems. Effective management of invasive conifers must therefore move beyond tree removal to include complementary restoration actions that address persistent abiotic and biotic legacies.

1 | Introduction

The invasion of nonnative tree species is one of the principal drivers contributing to ecosystem transformation, due to their capacity to simultaneously modify physical, chemical, and biotic components (Richardson et al. 2014; Rundel et al. 2014; Nuñez et al. 2021). Through their high biomass, longevity, and structural dominance, these species generate direct impacts

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by significantly altering the microclimate reducing light availability, changing canopy cover, and increasing litter (i.e., pine needles) accumulation (García et al. 2023). Such alterations in physical and environmental conditions produce indirect effects that affect biodiversity both aboveground and belowground (Moyano et al. 2023; Eckert et al. 2024; Yannelli et al. 2025). Even after invasion management, many of these impacts, especially the indirect ones, persist over time as *legacy effects*, understood as changes in abiotic or biotic conditions that remain after the invasion has been controlled and continue to influence community dynamics and ecosystem processes for years or decades, shaping the direction and rate of ecological succession (Suding et al. 2004; Cuddington 2011; Corbin and D'Antonio 2012; Reynolds et al. 2017). Plant invasion legacies may include shifts in nutrient dynamics (e.g., nitrogen mineralization rates or soil pH), shifts in fungal and bacterial community structure (Yannelli et al. 2025; Yi et al. 2025), as well as the persistence of allelopathic compounds that constrain future plant community assembly (Grove et al. 2012, 2015). Unlike the facilitative effects observed in pioneer species during natural successional processes, the legacies of woody invasive species tend to be disruptive, inhibiting succession and delaying functional ecosystem recovery (Corbin and D'Antonio 2012). Understanding the magnitude and duration of these effects is essential for designing effective restoration strategies that go beyond simple invader removal and incorporate complementary actions such as active restoration, modifications of soil conditions, and reduction of new disturbances (e.g., livestock exclusion) (Corbin 2025).

Nonnative trees, especially pines are one of the most invasive plant taxa in the world, with their invasive potential stemming from their widespread use in forest plantations and as ornamental species (Richardson et al. 1994; Essl et al. 2010, 2011; Kueffer et al. 2013; Nuñez et al. 2017). Successful global invasion by pines also results from a series of biological characteristics that increase their invasive potential, such as high reproductive rate, fast growth, and long-distance dispersal (García et al. 2018). Pines can indeed have severe impacts on ecosystem processes in the systems they invade, causing, for example, changes in water and fire regimes and reductions in local diversity (Simberloff et al. 2010; Van Wilgen and Richardson 2012). It has been documented that when nonnative trees (e.g., *Pinus* spp.) invade forested and treeless ecosystems (e.g., steppe, high mountains) they generate significant changes in microclimatic conditions and resource availability, a reduction in native plant diversity, a modification of soil biota, and an alteration of the trophic networks of the invaded ecosystems (García et al. 2023). However, the mechanisms underlying these changes are not yet fully understood. In particular, it remains unclear whether the observed impacts are mainly driven by competitive effects for resources or by environmental changes induced by the presence of pine, which could reduce the performance and survival of native species. Previous studies have shown that the accumulation of pine needles on the ground limits the germination and establishment of native plants (Taylor et al. 2016), while the dense canopy cover reduces light availability and dampens temperatures (García et al. 2018). For example, in the southern Patagonia steppe invaded by *P. contorta*, even at early stages of pine invasion a significant decline in plant richness and cover was observed, with continued to intensify with increasing pine canopy cover (Taylor et al. 2016; Franzese et al. 2017).

Due to the widespread impact of pine invasions on ecosystem functioning, various management and containment efforts have been implemented (Cuevas and Zalba 2010; Nuñez et al. 2017). However, a comprehensive assessment is still lacking on how these control techniques (i.e., mechanical, manual, or involving the use of fire) affect the local environment and whether they enable effective ecosystem restoration (Nuñez et al. 2017). There may indeed be significant challenges in this regard, as legacy effects can maintain suboptimal conditions for the recovery of native species even after pine removal (Cuddington 2011). This particularly limits the success of management efforts when the restoration goal is to reestablish low-stature, nonwoody native vegetation (Nuñez et al. 2017). Such legacies are most likely to develop in cases where invasive species cause local extirpations of resident species, alter resource pools, or interact with other aspects of global change (Corbin and D'Antonio 2012; Souza-Alonso et al. 2022), as is often the case for widespread conifer invasions (Nuñez et al. 2017). For example, the increased nutrient cycling rates resulting from pine invasion hindered the restoration of seminatural tussock grasslands and shrubland vegetation (Dickie et al. 2014). The legacy effect will also be driven by the invasion stage of the pines: Older invasive pine stands have lost much native species diversity, delaying the success of restoration goals (Nuñez et al. 2017).

In Chile, the invasion of *P. contorta* Douglas is concentrated in the southern regions, where it was introduced during the 1970s and 1980s to stop soil erosion caused by intensive agricultural activity in the 19th century and to promote the development of forestry production (Uribe et al. 2020). From these plantations, *Pinus contorta* has expanded in some ecosystems beyond the originally established areas, triggering an invasion process in which the plantations themselves act as the main source of propagules (Langdon et al. 2010). Two areas have been particularly affected by this invasion: Malalcahuello National Reserve in the Araucanía Region, where it has colonized the montane forest of *Araucaria araucana*, and the Patagonian steppe in the Aysén Region. In both ecosystems, significant impacts on microclimate and biodiversity have been documented (García et al. 2023, 2024). However, the extent of invasion varies markedly, being much more pronounced in the *A. araucana* forests, as the invasion in these ecosystems is much older than in the Patagonian steppe (Franzese et al. 2017; García et al. 2023). This situation represents a unique natural experiment, in which the same invasive conifer (*P. contorta*) is spreading across ecosystems that differ substantially in both climate and community structure, but also exhibit varying levels of invasion, primarily due to differences in the timing of introduction (Franzese et al. 2017; García et al. 2023). This contrast is particularly valuable, as it enables an assessment of how the invasion of a single species can affect both forested ecosystems and historically treeless environments, the latter being especially relevant from an evolutionary perspective, given that trees have never been part of their community structure (Rundel et al. 2014; Pauchard et al. 2016; Moyano et al. 2024).

The impacts of *P. contorta* on the ecosystems it invades have been widely documented (Cóbar-Carranza et al. 2014; Bravo-Monasterio et al. 2016; Franzese et al. 2017; Ulloa et al. 2023). In this context, previous studies in both ecosystems have shown that increasing *P. contorta* biomass generates significant effects on the richness

and abundance of native plant species, as well as on microclimatic variables (maximum soil and air temperatures) and soil properties, such as nutrient levels and pH (García et al. 2023). However, significant knowledge gaps remain regarding the persistence of these impacts on abiotic and biotic variables following management interventions, such as logging or other methods used to eliminate the invasive species, including mechanical or chemical culling of standing trees. Understanding whether environmental conditions and plant diversity recover after the removal of the invader is essential for assessing the presence of legacy effects and for guiding post-control restoration strategies. This question becomes particularly relevant when considering highly contrasting ecosystems, such as *Araucaria araucana* forests and the Patagonian steppe, which differ substantially in their evolutionary histories and community structure. Such differences raise critical questions about how the magnitude and persistence of invasion-driven impacts might shape ecosystem recovery trajectories following management interventions. In this context, we ask whether environmental variables and diversity return to conditions close to those prior to the invasion after 2 years of mechanical pine removal along a *P. contorta* invasion gradient in a montane forest (*Araucaria araucana* forest) and a Patagonian steppe ecosystem in southern Chile, or whether strong legacy effects on environmental and diversity variables slow down this recovery process. We propose the following hypothesis: The removal of the *P. contorta* canopy through management actions will promote a gradual recovery of microclimatic and physical conditions (direct impacts) toward those characteristics of noninvaded sites. However, the indirect effects of the invasion, such as reductions in the richness and abundance of native species, are expected to persist over time due to ecological legacies that limit the full recovery of biodiversity in both ecosystems (Figure 1), which would have direct implications for adaptive management strategies of nonnative species, requiring measures that not only focus on immediate eradication but also on the restoration of ecological processes and the prevention of long-term legacy effects.

2 | Methods

2.1 | Study Site and Historical Impacts

This study includes two contrasting Patagonian ecosystems that have been invaded by *Pinus contorta* for over 10 years. In the same plots of our study, previous research on invasion impacts has shown that increasing *P. contorta* biomass significantly decreases the richness and abundance of native species, causes major changes in microclimatic conditions (air and soil temperature), and soil properties (reductions in nitrogen, potassium, and pH). For more background on the study sites and invasion impacts, see García et al. (2023) (Figure 2a–c). The first ecosystem is an open forest dominated by the endangered tree *Araucaria araucana* (Molina) K. Koch (Yi et al. 2025), located on the southern slope of the Lonquimay volcano in the Malalcahuello National Reserve (38° 30′ S–71° 35′ W; 1420 m a.s.l), located in La Araucanía region in Chile. This area is characterized by a high annual rainfall, 3083 mm, mainly in the form of snow that is concentrated during autumn and winter and annual temperatures around 9°C (Franzese et al. 2017). Due to the presence of strong volcanic and glacial activity, this area has a unique topography that gives it a great variety of microclimates that significantly affect the spatial distribution of the species in this ecosystem (Peralta 1980). This site is a transition between an open forest dominated by *Araucaria araucana* and the subalpine steppe dominated by *Festuca scabriuscula* and with patches of *Nothofagus antarctica* and *Chusquea culeou* (Gajardo 1994). This transition from open forest to grassland has developed on young, nutrient-poor soils of volcanic origin, where microclimatic variations (e.g., differences in solar exposure,

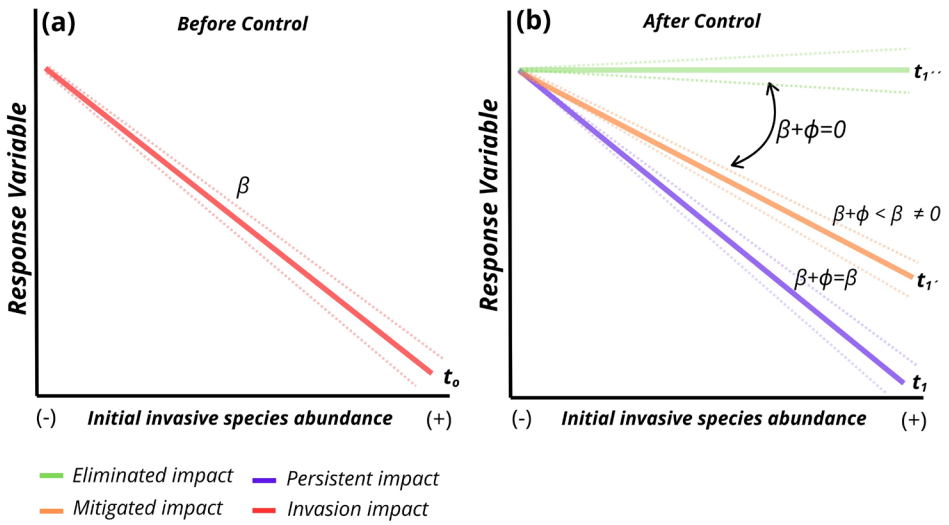

FIGURE 1 | Conceptual framework to evaluate the effect of invasive species removal on a response variable (abiotic, biotic) along a gradient of invasion density. Panel (a) shows the negative relationship between invasion density and a response variable (red line) under premanagement conditions, where the slope β reflects the magnitude of the invasion impact. Panel (b) illustrates the possible outcomes following the removal of the invader. The first scenario (green line) represents eliminated impact (t_1''), where the response variable fully recovers to no-invasions levels ($\beta+\phi=0$). The second scenario (orange line) corresponds to mitigated impact (t_1'), where the response variable shows partial recovery after the removal ($\beta+\phi<\beta\neq 0$). The third scenario (purple line) represents a persistent impact (t_1), where the response variable trend remains the same as under the invaded state ($\beta+\phi=\beta$), indicating a legacy effect of the invasion.**Note that although the framework is illustrated using negative slopes for simplicity, these relationships may also be positive depending on whether the invasive species increases or decreases the response variable prior to management.

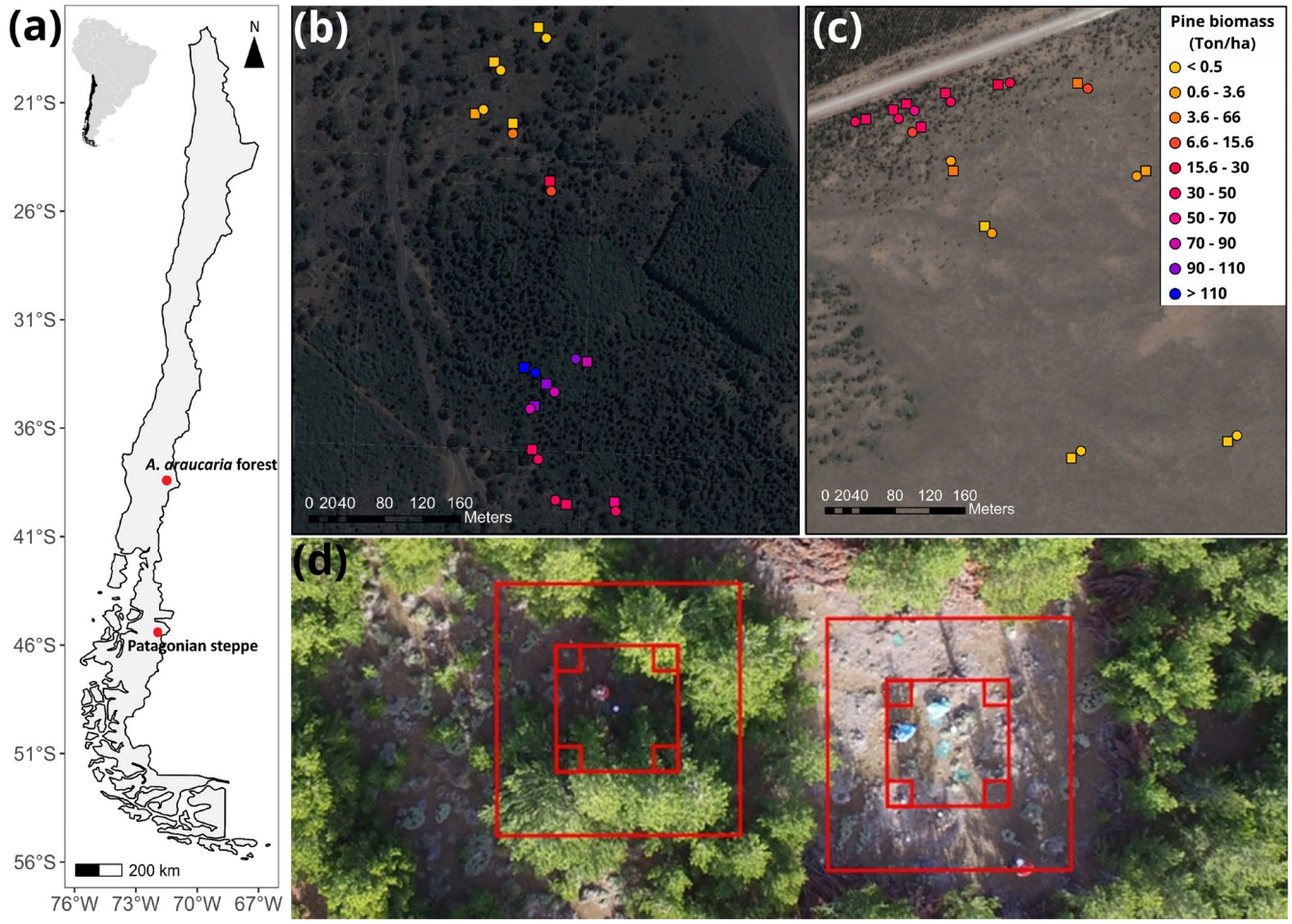

FIGURE 2 | Location and schematic representation of paired plots invaded (squares) and pine removal plots (circles) of *Pinus contorta* in *Araucaria araucana* forests and the Patagonian steppe. (a) Map showing the location of the study sites. Distribution of *P. contorta* plots based on initial pine biomass in *A. araucana* forests (b) and in the Patagonian steppe (c). (d) Diagram of the 100-m^2 plots under invaded and postremoval conditions. Also shown are the internal 25-m^2 subplots where microclimatic variables were measured, and the four 1-m^2 subplots used to assess species richness and abundance.

moisture, and frost regime) and edaphic heterogeneity constrain the regeneration of woody species, mainly toward the higher parts of the gradient (Franzese et al. 2017).

The second ecosystem is a Patagonian steppe located in the province of Coyhaique (45° 33′ S–72° 04′ W; 730 m a.s.l) in the region of Aysen, Chile. This steppe is characterized by a cold and dry climate, with total annual precipitation here around 450 mm, occurring mostly in winter. The mean annual temperature is around 7°C (Bravo-Monasterio et al. 2016). The vegetation is mainly composed of native species of the genus *Festuca* sp. and plants that grow in the form of cushions such as species *Bacharis magellanica* and *Acaena integrifolia* (Franzese et al. 2017). It is an area that is characterized by a strong anthropogenic disturbance associated mainly with livestock (Langdon et al. 2010).

2.2 | Invasion Removal Plots

To monitor the dynamics of the potential effects of removing *P. contorta* individuals on abiotic and biotic variables, we used an adaptation of the method proposed in the Global Invader Impact Network (GIIN) (Barney et al. 2015). To evaluate the effect of pine removal at each study site, 12 pairs of 100-m^2 plots ($n = 24$) were established in the spring of 2014 along an invasion gradient of *Pinus contorta* (Figure 2d). In each pair, one plot underwent mechanical pine removal (pine removal plot), whereas the other remained in an invaded condition (invaded plot).

The intensity of the *P. contorta* invasion at both sites was quantified by total *P. contorta* aerial biomass, which was obtained measuring all trees over 1 m of eight in each plot and its biomass was calculated with the functions developed for this invasive species by Cóbar-Carranza et al. (2014). The pine biomass in the gradient goes from 0 to 150 ton ha^{-1} in the *Araucaria araucana* forest site and a maximum pine biomass of 50 ton ha^{-1} for the Patagonian steppe (García et al. 2023), at the beginning of the measurements (Figure S1).

In each plot of 100 m^2, a central plot of 25 m^2 was installed where microclimatic measurements (i.e., soil temperature, air, soil moisture, PAR light) and leaf litter measurements were concentrated. Within these 25-m^2 plots, four 1-m^2 subplots were installed, which were used to measure the variables of richness and abundance of native and nonnative plant species (mostly herbaceous and shrub species) (Figure 2d). These plots were monitored starting in the

summer of 2014–2015 (December 2014–Febrary 2015 [0 years]) to obtain the preremoval measurements in all plots of each site (García et al. 2023). After one entire year of measurements, *P. contorta* removal was carried out in December 2015 in one plot of each pair (pine removal plots). Each pine individual inside the 100-m^2 plots was cut down at soil height using manual saws or chainsaws for larger diameters. All the residual biomass was removed from the interior of the plot, avoiding as much as possible damage to native vegetation and soil. This experiment was performed to test the effect of pine removal and not the usual collateral damage of traditional mechanical logging (Figure 3a–d). After the removal of the pines, environmental and diversity variables were measured annually over a 2-year period, during the summers (i.e., December–January) of 2016–2017 (1 year), 2017–2018 (2 years) to assess the legacy of the invasion.

2.3 | Environmental Measurements

To evaluate the legacy effect after the removal of the *P. contorta* invasion, a series of environmental variables, including soil and air temperatures, soil moisture, photosynthetically preremoval and other litterfall, were measured in the 25-m^2 plots. In each plot, soil moisture and temperature were recorded at a depth of 5 cm using Hobo Micro Station H21-002 sensors. Air temperature was recorded at 20 cm above the soil in each plot using the HOBO U23-001 Pro v2 Temp/HR sensor. These microclimatic variables were recorded at 1-h intervals from the plot installation in the summer of 2014–2015 through the summer of 2017–2018. To assess the effects of *P. contorta* removal on these variables and their ecological implications for native species recruitment, daily maximum, minimum, and average temperatures, as well as average humidity, from the preremoval growing season (summer 2014–2015) and the third post-control growing season (summer 2017–2018) were analyzed. The PAR (photosynthetically active radiation, in $\mu mol\, m^{-2} s^{-1}$) was measured during the growing season at midday (12:00–2:00 pm) with approximately four measurements per month (from December to February) using a luxmeter Apogee model MO-200.

To quantify the litter levels, a 20 × 20 cm quadrant was placed at the periphery of each 1-m^2 plot to avoid removing litter from

FIGURE 3 | Condition of the plots before and after the removal of *Pinus contorta* individuals in two contrasting ecosystems. Panels (a, b): Temperate *Araucaria araucana* forest. In this ecosystem, pine removal does not entail the complete elimination of vegetation, as native species such as *Chusquea quila* in the understory and *Araucaria araucana* in the canopy remain, preserving part of the original forest structure. Panels (c, d): Patagonian steppe. In this case, pine removal restores the landscape to its natural state, characterized by the absence of trees and the dominance of herbaceous vegetation (*Festuca* spp.), typical of the Patagonian steppe.

the main quadrants and thus prevent disturbance of recruitment patterns. All litter within the 20 × 20 cm quadrat was carefully removed for subsequent analysis. The samples were then dried at 70°C for 48 h and screened (2 mm) to separate the litter from the soil. The litter was separated and weighed, distinguishing between pine litter and other types of litter. Canopy cover and direct radiation (i.e., the proportion of potential solar radiation reaching the ground through canopy openings) under canopy were determined from a hemispheric photo taken in the center of each plot. To characterize the canopy cover of *P. contorta*, digital hemispheric photographs of the canopy were taken at a height of 50 cm above the center of each plot. A Nikon f 7.4 7 mm fisheye lens (with an orthographic projection of 180° field of view) mounted on a Nikon Coolpix 5000 digital camera (Nikon Corporation, Tokyo, Japan) was used. Photographs were taken under cloudy sky conditions or at the end of the day to avoid direct sun exposure. In addition, two points were underexposed to increase the contrast between sky and foliage (Zhang et al. 2005). Canopy cover was calculated for each plot using Gap Light Analyzer software v.2.0.

2.4 | Diversity Measurements

To evaluate the legacy effects of *P. contorta* on the biodiversity of both ecosystems, the richness and abundance of both native and nonnative plants were measured. In each plot, the richness and abundance of native and nonnative plant species were determined using the average of four 1-m^2 subplots installed in the corners of the 25-m^2 plot. The classification of species as native or nonnative was based on the *Catalogue of the Vascular Plants of Chile* (Rodríguez et al. 2018).

2.5 | Statistical Analysis

To evaluate whether the mechanical removal of *P. contorta* leads to short-term recovery or whether legacy effects persist, we analyzed the effect of pine removal across the invasion gradient on both environmental conditions and plant diversity. Linear mixed models (LMMs) were used for environmental variables (soil moisture and temperature, air temperature, photosynthetically active radiation [PAR], canopy cover, and pine litter), and generalized linear mixed models (GLMMs) were used for the richness and abundance of native and nonnative plant species. In both cases, "treatment" (invaded vs. pine removal) was included as the main predictor and the ID of the paired plots was included as a random effect to account for spatial variation within study sites. It is important to note that although *P. contorta* biomass is zero in the pine removal treatment after management, the pre-removal biomass gradient was used as an indicator of invasion history or intensity. Thus, biomass is interpreted as a continuous proxy of past invasion impacts rather than a posttreatment covariate, allowing us to assess whether initial invasion conditions explain the short-term environmental and biological responses observed after removal.

LMMs were fitted with the *lmer* function from the lme4 package (Bates et al. 2015), and model assumptions (normality, homogeneity of variance and linearity) were verified using the *performance* package (Lüdecke et al. 2021). GLMMs were fitted with the *glmmTMB* package (Brooks et al. 2017), assuming a Poisson distribution with log link function. Zero inflation and overdispersion were assessed using the *DHARMa* package (Hartig and Hartig 2017). To determine whether the slope associated with treatment varies significantly along the *P. contorta* biomass gradient, we used the *emmeans* package (Lenth 2016), which allows comparison of marginal effects and the evaluation of the significance of slopes for each predictor (Δβ, i.e., the difference between slopes). A nonsignificant difference in slope between invaded and removal plots would indicate the persistence of a legacy effect of the invasion, whereas a significant difference that resembles the noninvaded state would suggest recovery after removal. Predicted values were obtained using the *predict* function in R and visualized with *ggplot2* (Wickham 2008) to illustrate trends across the invasion gradient.

3 | Results

3.1 | Legacy Effect of *Pinus contorta* Invasion

As hypothesized, the removal of *Pinus contorta* in both ecosystems had a significant effect on some of the direct impacts caused by the invasion, particularly on microclimatic variables (e.g., maximum and minimum soil temperatures, maximum air temperatures, soil moisture) and structural components (canopy cover and pine litter accumulation). However, the recovery of

TABLE 1 | Estimated values and *p* values for each variable and study site, resulting from slope comparisons between invaded and pine removal plots.

Variable delta	Araucana forest		Patagonian steppe	
	Estimate	*p*	Estimate	*p*
T° max soil	−4.963	**<0.001**	1.702	***0.007***
T° min soil	8.931	**<0.001**	1.336	*0.434*
Soil moisture	0.051	0.497	0.114	**<0.001**
T° max air	0.776	***0.013***	0.902	0.213
T° min air	1.944	***<0.001***	0.356	***0.040***
Canopy cover	−0.203	***<0.001***	88.530	***<0.001***
PAR	41.190	***0.048***	49.480	***0.004***
Pine litter	0.170	0.973	21.396	**<0.001**
Native richness	−0.125	0.788	−0.072	0.657
Native abundance	−3.791	0.180	−0.152	0.079
Nonnative richness	0.062	0.563	−0.282	0.434
Nonnative abundance	−0.185	0.825	−0.844	***0.001***

Note: Comparisons were made using the estimated marginal means method for both models (LM and GLMM). Variables that changed between treatments are shown in bold italics.

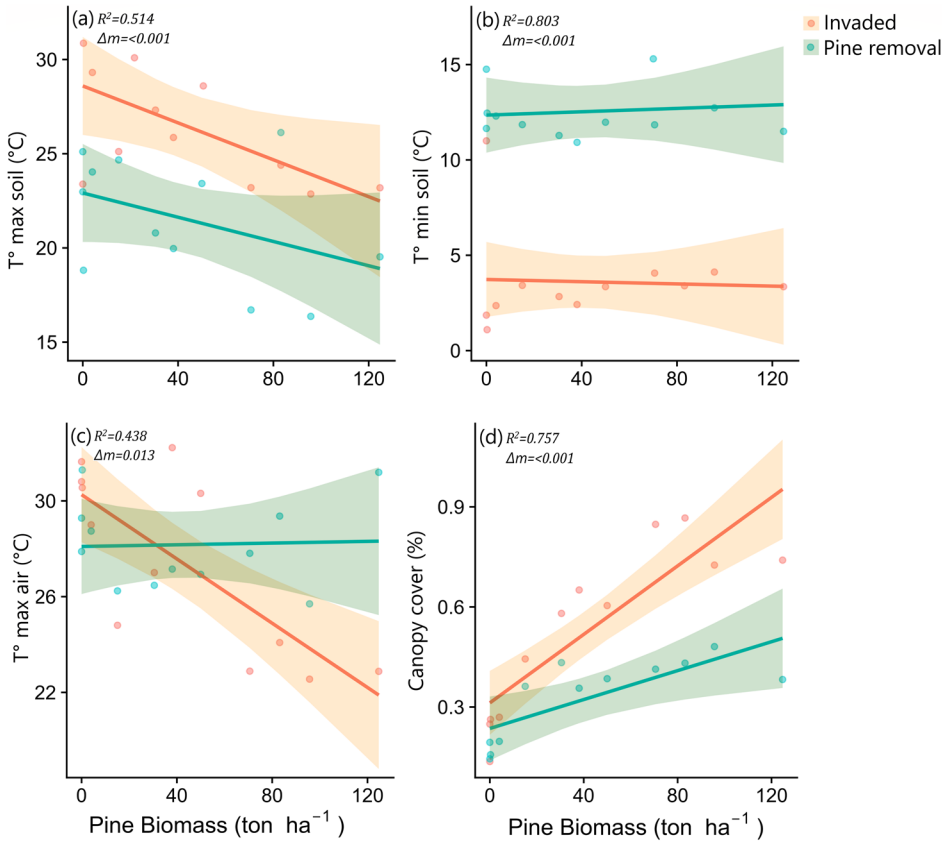

FIGURE 4 | Maximum and minimum soil temperature (a, b), maximum air temperature (c), and canopy cover (d) in *Araucaria araucana* forest as a function of the amount of pine biomass (in tons ha^{-1}) before removal (orange/2015) and after removal (green/2017). Dots indicate individual measurements, lines are linear mixed model predictions, with shaded areas for confidence interval. R^2 values correspond to marginal R^2 that includes only the effect of predictors (biomass and removal/nonremoval). Δm indicates the p value for the difference in slopes between invaded and pine removal plots.

native plant richness and abundance was clearly delayed after removal, with no signs of improvement observed 2 years after the management intervention (Tables S1 and S2).

In *Araucaria araucana* forests, when estimating differences between treatments along the biomass gradient ($\Delta\beta$), the *pine removal* treatment produced a decrease in maximum soil temperature ($-8.62°C \pm 3.11°C$) and an increase in minimum soil temperature ($+5.68°C \pm 0.79°C$) compared to invaded plots ($\Delta\beta < 0.001$) (Table 1; Figure 4a,b). Regarding air temperature, pine removal significantly increased maximum temperature ($+0.78°C \pm 0.13°C$; $\Delta\beta$, $p = 0.013$), resulting in previously highly invaded plots becoming similar to uninvaded ones (Table 1 and Figure 4c). Structurally, canopy cover showed a less pronounced slope after removal (Figure 4d). Nevertheless, the removal of *P. contorta* biomass did not promote a recovery in native plant richness or abundance (Table 1; Figure 5a,b).

In the Patagonian steppe, biomass removal increased maximum soil temperature by $1.70°C \pm 0.34°C$, bringing heavily invaded plots closer to values characteristic of plots with near-zero *P. contorta* biomass ($\Delta\beta$, $p = 0.007$) (Table S1; Figure 6a). A slight increase in minimum air temperature was also observed ($+0.62°C \pm 0.39°C$), although it did not reach levels found in uninvaded plots ($\Delta\beta$, $p < 0.023$) (Table S1; Figure 6c). Soil moisture significantly increased in removal plots, reaching values similar to those characteristic of plots with near-zero *P. contorta* biomass ($\Delta\beta$, $p < 0.001$) (Tables S1, S2; Figure 6b). Finally, *P. contorta* removal significantly reduced pine litter (-1.262 ± 0.87 g/m^2), also approaching uninvaded levels ($\Delta\beta$, $p < 0.001$) (Table S1; Figure 6d).

As in *A. araucana* forests, pine removal in the Patagonian steppe did not significantly enhance the recovery of native plant richness or abundance (Table S1, Figure 7a,c). However, a slight increase in the richness and abundance of nonnative plants was observed (Table S1, Figure 7b,d).

4 | Discussion

Our results highlight that the invasion impacts persisted, at least in the short term, particularly in the Patagonian steppe, where drier soils, greater litter accumulation, and altered light regimes were still being observed in the managed plots. In contrast, invasion legacies in the *Araucaria araucana* forest were less pronounced and were mainly associated with changes in soil temperature amplitude. In both ecosystems, we detected a short-term legacy effect on the richness and abundance of native plant species, which showed no signs of recovery even two growing seasons after removal.

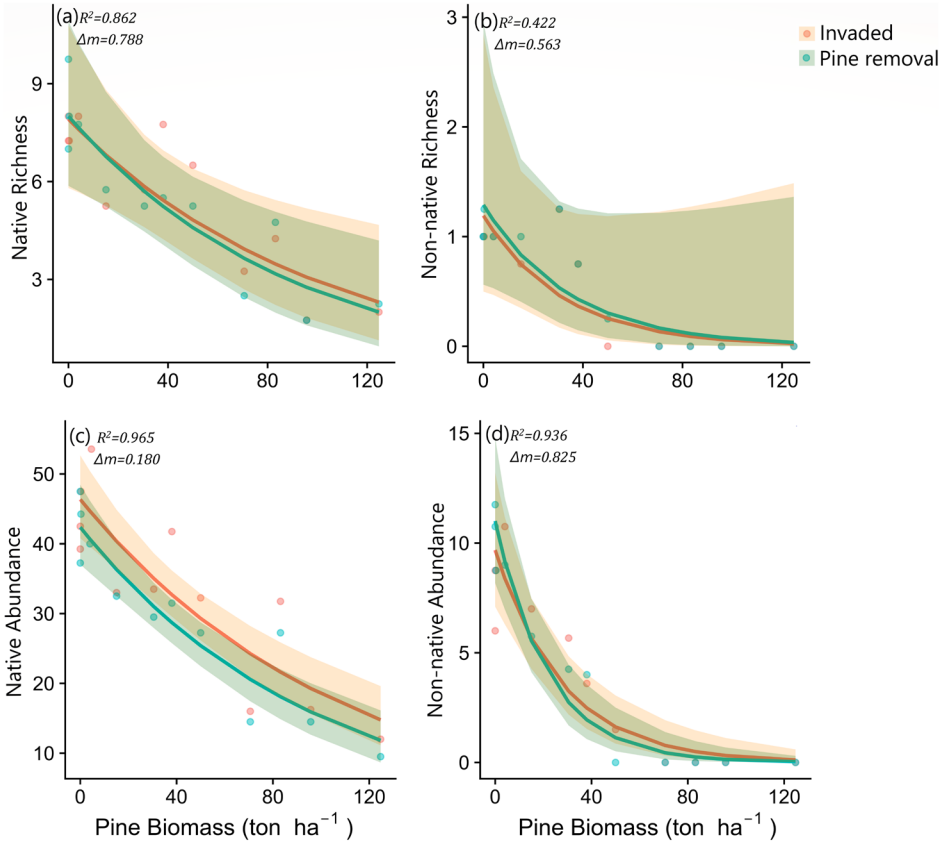

FIGURE 5 | Richness and abundance of native (a, c) and nonnative (b, d) plants in *Araucaria araucana* forest as a function of the amount of pine biomass removed (in tons ha^{-1}) before removal (orange/2015) and after removal (green/2017). Dots indicate individual measurements, lines are generalized linear mixed model predictions, with shaded areas for confidence interval. R^2 values correspond to marginal R^2 that includes only the effect of predictors (biomass and removal/nonremoval). Δm indicates the p value for the difference in slopes between invaded and pine removal plots.

Our results show that removing *Pinus contorta* biomass along the invasion gradient does not immediately or at least in the 2 years evaluated in this study cause a detectable recovery of native biodiversity in either ecosystem (Taylor et al. 2016; García et al. 2018). In fact, native-species richness was consistently lower across the entire invasion gradient and did not differ between pine removal and invaded plots either before or after management. This decline in native species richness—which was also reflected in a reduction in native species abundance—could indicate a strong legacy effect of pine invasions following removal, at least in the short term (Cuddington 2011; Nuñez et al. 2017).

Legacy effects of *P. contorta* on native biodiversity may be linked to the persistence of pine litter in removal plots. Although total litter mass declined in some plots following tree removal (especially in the Patagonian steppe), the mass of pine litter itself remained constant over time. Because of its chemical composition, pine litter has been shown to take longer to degrade than native tree litter (Araujo and Austin 2015). Consequently, it might remain present on the soil for multiple years and limit new germination of native species, and thus the recovery of native diversity. In our study system, plots with the highest initial pine biomass exhibited the greatest loss of native biodiversity; in those sites, diversity was already severely reduced (García et al. 2023), so recovery would largely depend on recruitment from the seed bank or recolonization by pioneer native species. Moreover, the potential role of litter in limiting native regeneration highlights the importance of considering post-removal litter management. Several studies have shown that the persistence of thick pine litter layers can reduce light availability, alter soil temperature, impede seed–soil contact, and ultimately suppress the germination of native species (Araujo and Austin 2015; Nsikani et al. 2018). In systems where invasive conifer litter accumulates slowly and decomposes at reduced rates, removal of this litter layer (either manually or through low-intensity prescribed burning) has been proposed as a strategy to facilitate native seedling emergence and improve restoration outcomes (Elgersma and Ehrenfeld 2011; Nsikani et al. 2018). Thus, in heavily invaded sites, such as those with high initial pine biomass in our study, active litter removal could enhance germination and early recruitment, helping to overcome legacy barriers and accelerate recovery of native plant diversity.

It could be hypothesized that by opening the forest canopy through pine removal, litter decomposition rates would increase due to higher radiation and higher temperature (Portillo-Estrada et al. 2016). However, in our study system, this mechanism appears to play only a limited role, as our results show no significant effect of the amount of pine biomass removed on temperature patterns. This is particularly evident in the soil, where strong positive feedback would be expected to generate greater warming (and thus promote higher decomposition rates), which was not observed. Such a limited effect of pine biomass on microclimate

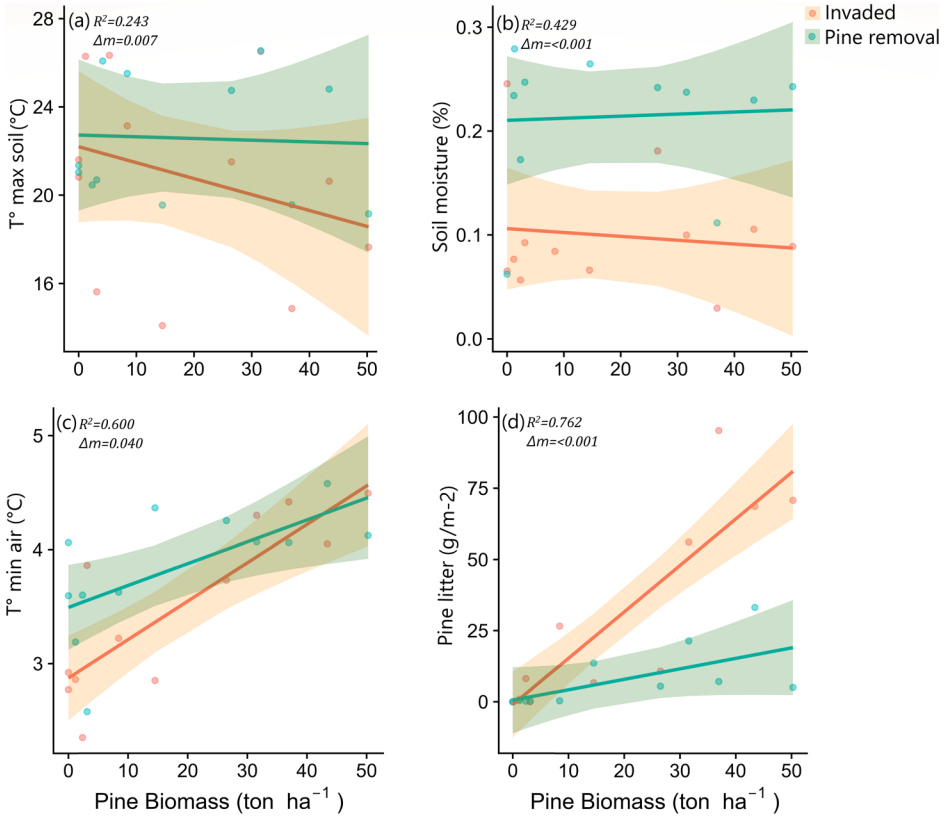

FIGURE 6 | Maximum soil temperature (a), soil moisture (b), minimum air temperature (c), and canopy cover (d) in Patagonian steppe as a function of the amount of pine biomass removed (in tons ha^{-1}) before removal (orange/2015) and after removal (green/2017). Dots indicate individual measurements, lines are generalized linear mixed model predictions, with shaded areas for confidence interval. R^2 values correspond to marginal R^2 that includes only the effect of predictors (biomass and removal/nonremoval). Δm indicates the p value for the difference in slopes between invaded and pine removal plots.

is surprising yet is backed up partially by previous work showing only small temperature differences between different forest stands (Porté et al. 2004). We propose that simply reducing canopy cover by removing pine biomass is insufficient, in the short term, to restore native communities in our study system, because multiple legacy effects of the invasion persist. These legacies are not limited to the residual litter layer; they also include a depleted seed bank, low propagule pressure, and other biotic constraints that limit the ability of native species to germinate, recruit, and recolonize (Cuddington 2011; Corbin and D'Antonio 2012). Although canopy opening modestly improved abiotic conditions (warmer soils and slightly higher moisture), these improvements did not offset the combined biotic and structural legacies.

Moreover, the prolonged presence of *P. contorta* likely altered the soil and litter microbiome, including ectomycorrhizal fungi, soil microbes, and soil fauna associated with pine stands. Pines are known to coinvade with their fungal symbionts, reshaping soil communities and nutrient dynamics in ways that can persist for years (Dickie et al. 2014; Policelli et al. 2019). In addition, pine needles harbor diverse microbial assemblages (Steel et al. 2022; Zhao et al. 2025) that can be transferred to seedlings via the litter layer (Meyer et al. 2022), potentially generating plant–phyllosphere feedbacks that reduce native recruitment (Pajares-Murgó et al. 2025). Together, these microbiome-driven legacies may reinforce plant–soil and plant–phyllosphere feedbacks that are unfavorable for native species (van der Putten et al. 2016), thereby persisting long after biomass removal and further hindering the recovery of native vegetation.

It is important to consider that, beyond the effects of litter accumulation observed in plots, where *P. contorta* was removed, other relevant factors not measured in this study may also play a role, many of which occur belowground. Previous research has shown that the invasion of species such as *Berberis thunbergii* can directly alter soil microbial communities, indirectly affecting the recruitment of native species (Elgersma and Ehrenfeld 2011). Additionally, the decomposition of residual litter has been found to modify nitrification rates and nutrient availability in the soil (Afzal et al. 2023). In some cases, litter from invasive species releases polyphenols and tannins, compounds known to inhibit the germination of native species and alter nitrogen cycling (Zhang et al. 2021). Furthermore, the invasion of *Acacia saligna* has been shown to negatively impact soil bacterial communities, and even after management interventions, these communities often exhibit slow recovery, thereby limiting nutrient availability (Yannelli et al. 2025).

For nonnative plants, pine removal produced no significant changes in *A. araucana* forests, whereas in the Patagonian steppe, it led to increases in richness and abundance, chiefly in plots with low initial *P. contorta* biomass. Where the initial biomass was high, this effect disappeared. This pattern aligns with evidence showing that nonnative species can act as pioneer

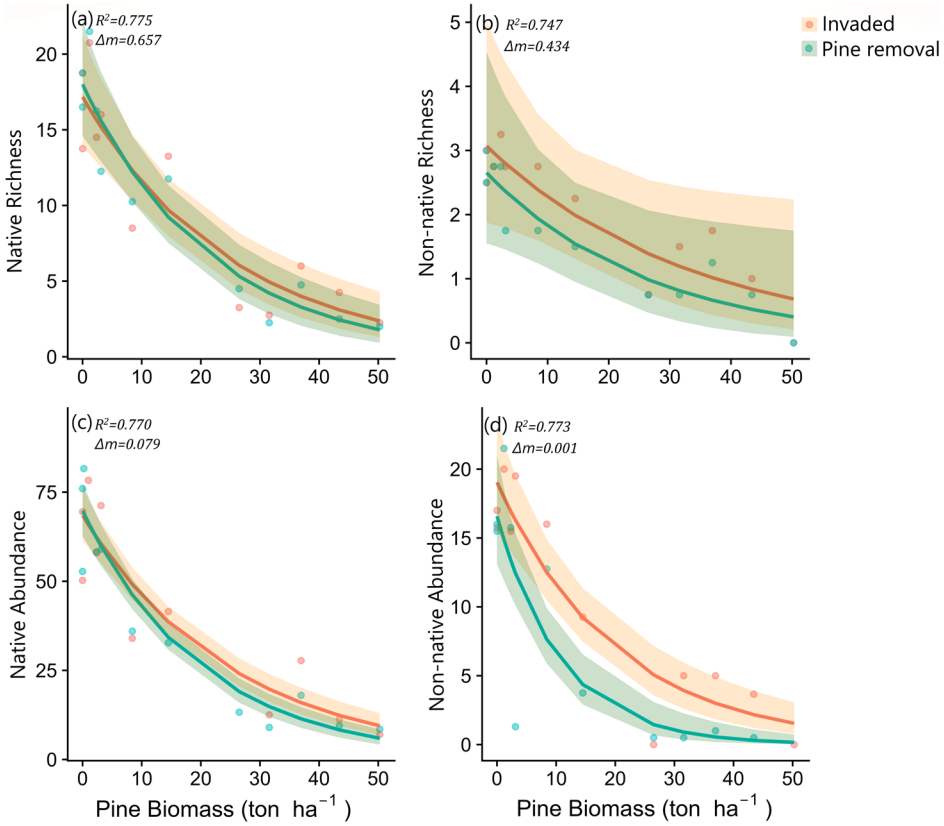

FIGURE 7 | Richness and abundance of native (a, c) and nonnative (b, d) plants in Patagonian steppe as a function of the amount of pine biomass removed (in tons ha^{-1}) before removal (orange/2015) and after removal (green/2017). Dots indicate individual measurements, lines are generalized linear mixed model predictions, with shaded areas for confidence interval. R^2 values correspond to marginal R^2 that includes only the effect of predictors (biomass and removal/nonremoval). Δm indicates the p value for the difference in slopes between invaded and pine removal plots.

colonizers after conifer removal, particularly in treeless ecosystems (Cuevas and Zalba 2010). Combined with the negative effects on native species diversity, these results suggest that delaying the management of invasion fronts till pine biomass is large can shift the balance in the understory after the management in favor of nonnative species (Dickie et al. 2014; Nuñez et al. 2017). These conclusions back earlier recommendations that it is key to tackle pine invasions before they progress too far (Cuevas and Zalba 2010; Nuñez et al. 2017), as waiting longer not only increases the physical and economical investment needed for management (Simberloff et al. 2010), it also decreases the short-term benefits for native biodiversity through an enhanced legacy effect, as shown here (Nuñez et al. 2017). In addition, maintaining standing pines (especially large individuals) creates residual influences in removal plots, as these remaining trees continue to cast shade, modify the surrounding microclimate, act as propagule sources that facilitate reinvasion, and sustain conditions that can hinder the arrival and establishment of native species in managed areas. Our results highlight the complex management decisions associated with the management of pine invasions in South America, even though management at the stand scale seems simple compared to that for many other invasive species, especially given that adult trees do not resprout after being cut down (Pauchard et al. 2015). The straightforward removal of pine biomass does, however, not ensure, at least in short-term periods, an increase in native biodiversity. On the other hand, by having a direct effect on abiotic conditions, management can facilitate the recovery of the native vegetation. However, the legacy effect of pine invasions seems unavoidable, especially in consolidated pine invasions, where native species have already been displaced. Furthermore, these managed stands may be more favorable for other nonnative species which can become extremely abundant after harvesting (García et al. 2024). In particular, we observed that *Rumex acetosella* and *Cerastium arvense* consistently increased in abundance following the removal of *Pinus contorta* in both ecosystems. Both species exhibit ruderal strategies, which allow them to rapidly colonize disturbed environments and take advantage of the more open conditions generated by pine removal. As has been said before in this and other literature, active restoration measures might thus be necessary to limit new invasions by pines or other nonnative species (Pauchard et al. 2015; Souza-Alonso et al. 2022). Long-term follow-up of the experimentally managed sites in this study can shed light on the question if the balance will tilt more toward native or nonnative species (with the former being shown in a comparable experiment, Cuevas and Zalba 2010), or if new pine seedlings germinating from seeds in the seed bank or from nearby plantations would take over again (Pauchard et al. 2015). We thus strongly recommend managers to act as early as possible to limit costs and efforts of pine removal and consequent restoration.

Author Contributions

E.F.-L. led the formal analysis, data curation, and investigation; contributed to methodology development; and wrote the original draft.

R.A.G. and A.P. contributed to the conceptualization and methodology and participated in writing and reviewing the manuscript. J.J.L. contributed to conceptualization and participated in writing and reviewing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Relationship between *Pinus contorta* biomass (ton ha^{-1}) and invasion level in two ecosystems: *Araucaria araucana* forest (left) and Patagonian steppe (right). **Table S1:** Estimated coefficients and *p*-values from linear mixed-effects models evaluating the effects of *Pinus contorta* biomass, treatment (invaded vs pine removal), and their interaction on microclimatic and structural variables in *Araucaria araucana* forest and *Patagonian steppe*. **Table S2:** Estimated coefficients and *p*-values from linear mixed-effects models evaluating the effects of *Pinus contorta* biomass, treatment (invaded vs pine removal), and their interaction on native and nonnative plant richness and abundance in *Araucaria araucana* forest and *Patagonian steppe*. **Table S3:** Estimated values and *p*-values for each variable and study site, resulting from slope comparisons between invaded and pine removal plots. Comparisons were made using the estimated marginal means method for both models (LM and GLMM). **Data S1:** jvs70110-sup-0003-DataS1.xlsx.