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ORIGINAL ARTICLE

Seed bank responses after clearcutting *Pinus patula* plantations in Andean high montane areas

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Abstract

Clearcutting exotic plantations favours natural regeneration processes in which seed banks may play an important role. In Andean high montane areas, after *Pinus patula* clearcutting, changes in soil pH and litter lead to increased fauna and flora biodiversity. However, the impact of these changes on seed banks remains unknown. The aims of the present study were to understand how seed bank richness, abundance, and composition changes after *P. patula* clearcutting, and to identify the role of aboveground cover, pH and litter cover on these seed bank variations. The study was conducted in three areas with different post-clearcutting ages (0, 2.5, 4.5 years), a *P. patula* plantation and in a high Andean forest patch. All these sites were located between 3 033 and 3 100 m.a.s.l. Seed bank abundance, richness and the number of seeds of the ten most abundant species increased in areas with 2.5 and 4.5 years after clearcutting. Moreover, seed bank composition was different among study areas. These changes were related to increasing aboveground vegetation cover and soil pH, and to decreasing litter cover. Seed banks contributed almost exclusively to the recovery of some herbaceous species; we recorded only one tree species recruit from the seed banks (*Baccharis latifolia*) in the forest soils; therefore, the natural regeneration processes may be constrained. Our results highlight the need to implement active restoration to accelerate high montane forest recovery in areas previously covered with pine tree plantations.

Keywords: Clearfelling; pine needle litter; *Pinus* sp.; secondary succession; soil pH.

Introduction

Globally, the loss of natural forests is, in many cases, compensated for by the planting of exotic tree species. About 131 million hectares are planted with one or two species (FAO, 2020), of which more than 22 million consist mainly of *Pinus* spp. monocultures (Stanbury *et al*., 2018). If current trends continue, exotic plantations could make up almost a quarter of all forest cover by 2100 (Brockerhoff *et al*., 2013). A critical situation is seen in South America where 99 % of the trees planted are exotic, and they represent 2 % of the forested area (FAO, 2020). Pine species, which have been extensively planted, have become one of the main threats to the conservation of South American native ecosystems (Cuevas & Zalba, 2010; Torres *et al*., 2018). Non-native *Pinus* spp. and *Eucalyptus* spp. tree plantations sustain less diversity than native ones (Jadán *et al*., 2019; Valduga *et al*., 2016) and alter biotic and abiotic conditions which may impede natural regeneration (Baruch *et al*., 2016). In particular, *Pinus* spp. plantations accumulate a thick and dense litter layer of needles, rich in lignin, that takes a long time to degrade (Tulande-M. *et al*., 2018a). This litter layer acidifies the soil (León & Vargas, 2007) and reduces or inhibits native species germination and establishment (Valera-Burgos *et al*., 2012; Bueno & Baruch, 2011).

There is a growing global interest in restoring areas of commercial pine plantations back to native ecosystems (Stanbury *et al*., 2018). The role of recruitment of native species from seed banks has been considered a key aspect when choosing an ecological restoration strategy to be implemented in areas planted with exotic *Pinus* spp. (Galloway *et al*., 2017). In this context, clearcutting constitutes the first stage to restore native ecosystems (Cuevas & Zalba, 2010, but see Torres *et al*., 2018). The removal of non-native pines increases the intensity of light, soil moisture content (Cuevas & Zalba, 2010; Eycott *et al*., 2006), and pH (Galloway *et al*., 2017), which might promote the recovery of native species richness and cover (Torres *et al*., 2018). Moreover, these conditions favour species colonization processes, in which the seed bank may have an important role (Bedoya-Patiño *et al*., 2010). However, in high montane forests no seed bank studies have been carried out after clearcutting exotic plantations. Nevertheless, results of experiments examining the effect of *Pinus patula* thinning on seedling emergence from the seed bank (Corredor & Vargas, 2007; León & Vargas, 2007) suggest that it may play a role in forest recovery.

To evaluate the contribution of seed banks to vegetation recovery, it is necessary to consider that they may reflect changes occurring in the ecosystem after the removal of *P. patula* trees (Borda & Vargas, 2011). For instance, in native high montane forests, seed banks mirror processes occurring in the current or preceding aboveground vegetation (Cantillo *et al*., 2008). However, the role of the mechanisms underlying seed bank responses, such as aboveground cover, soil pH, and litter cover are poorly understood (Eycott *et al*., 2006; Egawa & Tsuyuzaki, 2013). In

Andean high montane areas, shifts in quality and quantity of litter cover and physicochemical soil features have been recorded after clearcutting of *P. patula* plantations (Tulande-M. *et al*., 2018a). These changes have altered species composition and increased their richness and abundance (Tulande-M. *et al*., 2018a; Tulande-M. *et al*., 2018b), but their effects on the seed bank remain obscure.

The Parque Forestal Embalse del Neusa, in the Colombian Andes, has been subjected to removal of exotic pines by the environmental authority Corporación Autónoma Regional de Cundinamarca (CAR). Subsequently, the organization started an ecological restoration program to convert these plantations to the original high montane Andean forest. Since 2014, as part of a cooperation agreement, CAR and Pontificia Universidad Javeriana established permanent plots to monitor changes in community composition and structure after pine plantation removal (Tulande-M. *et al*., 2018b). Therefore, the site offers a unique opportunity to study how the seed bank changes in post-pine systems.

We evaluated whether seed bank richness, abundance, and composition change after clearcutting *P. patula* plantations, and what could be the role of aboveground cover, soil pH, and litter cover on these seed bank changes. We assessed the seed bank characteristics of three areas with different ages post clearcutting of *P. patula*, and compared them to those of a high Andean forest patch, located at 3 033-3100 m.a.s.l. We hypothesized that after the clearcutting of *P. patula* plantations, previously recorded increases in vegetation cover and soil pH and a decrease in exotic species litter cover (Tulande-M. *et al*., 2018a; Tulande-M. *et al*., 2018b) are reflected in a rise in seed bank richness and abundance, as well as on changes in species composition.

Materials and methods

Study site

The survey was conducted in a forest reserve, the Parque Forestal Embalse del Neusa (PFEN), Cundinamarca, Colombia (**Fig. 1**). The reserve is located at 3 000-3400 m.a.s.l on the eastern Andean Cordillera of Colombia (5° 09'30.2"N, 73° 56'24.2" W). The rainfall regime in this area is bimodal; the first rainy season occurs between April and May and the second between October and November. The average precipitation is 1 025 mm/year and the average annual temperature is 10.5 °C (Tulande-M. *et al*., 2018a).

The PFEN is humid (aridity index >35), according to the De Martonne climatic classification (IGAC, 2014). This classification is based on

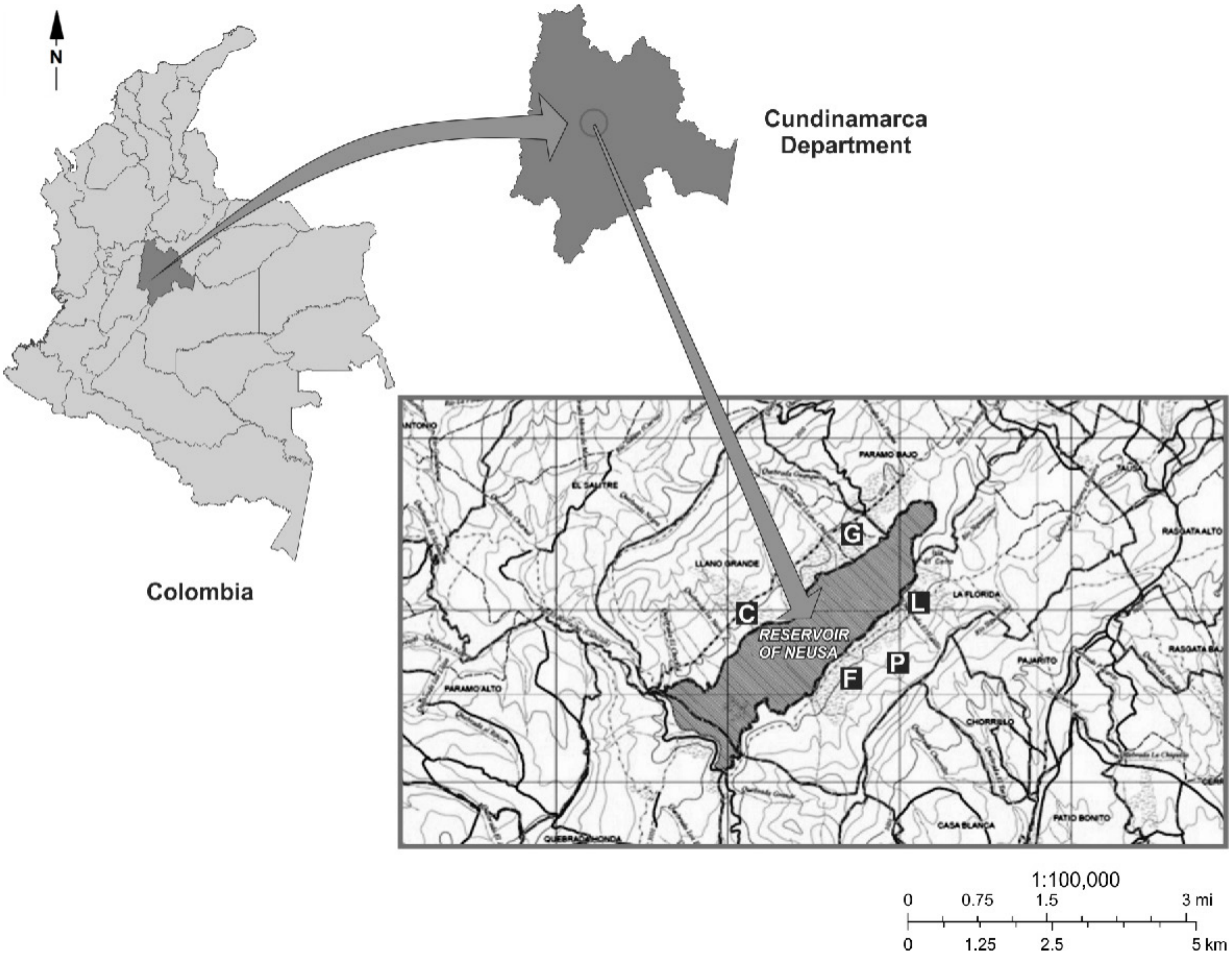

Figure 1. Location of Parque Forestal Embalse del Neusa, Colombia. Study sites are labelled as: L (Laureles, 0-8 months after clearcutting), C (Chapinero, 2.5 years after clearcutting), G (Guanquica, 4.5 years after clearcutting), P (*Pinus patula* plantation), and F (native forest).

geographical criteria and, by using an aridity index, it enables the classification of the climate of areas in which humidity is an important factor (IGAC, 2014). The index is applicable locally and depends on local average annual rainfall (mm), average annual temperature (°C), precipitation in the driest month, and the temperature of that month (IGAC, 2014). Furthermore, soils of the study site are classified as Silty Clay Loam by their textural class (Soil Science Division Staff, 2017), with prevalence of silt and clay (Tulande-M. *et al*., 2018a) and low concentrations of calcium, magnesium, potassium, and sodium (Tulande-M. *et al*., 2018b). The area shows slope mean values between 7.3 and 11 (Tulande-M. *et al*., 2018a).

The PFEN forest reserve has undergone a major process of transformation but still exhibits degradation characteristic of high montane Andean forest ecosystems of Colombia (Contreras-Rodríguez *et al*., 2011). Between the 1950s and 60s, a *P. patula* plantation was established around an artificial reservoir in the PFEN to control erosion and avoid sedimentation that could affect the waterbody (Contreras-Rodríguez *et al*., 2011). These plantations never received silvicultural management which caused wildfires that led to the disappearance of most of the few remnants of native forests (Contreras-Rodríguez *et al*., 2011). For this reason, in 2009 the environmental authority Corporación Autónoma Regional de Cundinamarca decided to carry out a forest harvesting program based on clearcutting, followed by an ecological restoration initiative to convert these areas to the original high montane Andean forest (Tulande-M. *et al*., 2018a). As a result of this clearcutting process, there are areas with variable post clearcut ages, but with similar climatic and edaphic properties.

We selected three areas with different ages after clearcutting: 1) Laureles (0-8 months after clearcutting), 2) Chapinero (2.5 years after clearcutting), and 3) Guanquica (4.5 years after clearcutting). In addition, we selected an extant *P. patula* plantation and a high montane Andean forest patch (i.e., remnant of montane rain forest according to Holdridge *et al*. (1971)). The area with an age of 0-8 months after clearcutting is almost lacking in any vegetation cover and only some dominant species have been recorded, specifically, *P. patula*, *Phytolacca bogotensis*, *Vallea stipularis, Hypochaeris radicata*, and *Rubus* spp. The area with an age of 2.5 years after clearcutting is dominated by *Galium hypocarpium*, *P. bogotensis*, *Muehlenbeckia tamnifolia*, *Rubus* spp., *Anthoxanthum odoratum*, *H. radicata*, *Holcus lanatus*, and *Rumex acetosella*. The last 5 species are also dominant in the area with 4.5 years after clearcutting. In the latter, *Ageratina gracilis* and *Digitalis purpurea* are also dominant. In the exotic plantation the only species recorded was *P. patula*. In contrast, the high montane Andean forest patch is dominated mainly by *Weimannia tomentosa*, *Bucquetia glutinosa, Clusia multiflora, Diplostephium rosmarinifolium*, *Drimys granadensis*, *Gaiadendron punctatum*, and *Viburnum triphyllum* (Suppl. 1). Further information about the study site is provided in Moreno *et al*. (2018) and Tulande-M. *et al*. (2018a). In each area we established nine (10 x 10 m) plots randomly distributed over a twelve-hectare stand in 2014 (Moreno *et al*., 2018). All plots were located in zones out of postfire areas.

Soil seed banks sampling and characterization

Inside each 10 x 10 m plot, we randomly located one quadrant (5 x 5 m) and divided each quadrant into a grid of 1 x 1 m. Within each grid, ten sections were randomly selected for soil seed bank sampling, and one soil core was extracted per section (Basto *et al.*, 2018). Soil sampling was carried out in September 2014, namely at the end of the dry season. Soil cores, 2.5 cm in diameter, were taken up to 20 cm deep (Basto *et al.*, 2018). The samples were split at 10 cm deep intervals for processing and analysis. The total number of soil samples for the seed bank study was 900. On the basis of previous research in our study area (Tulande-M. *et al.*, 2018a,b), we carried out an independent soil pH analysis to investigate its effects on seed banks. At each seed bank sampling point another core was taken to measure pH. Each soil sample, both for seed bank and pH analyses, was taken excluding leaf and needle litter or plant roots (Œycott *et al.*, 2006). To measure soil pH, each core was sieved (2 mm) and a soil suspension was prepared (1:2 soil/distilled water). The suspension was stirred at 0, 15, and 30 min, and soil pH was measured with a digital pH-meter equipped with a glass electrode (Lutrón PH-207HA).

Seed bank characterization took place following Thompson *et al*. (1997). First, vegetative plant parts were removed from soil samples. Second, the samples were sieved (4.75 mm, 2 mm, and 600 μm) and spread in 37.5 x 22 x 6 cm plastic germination trays in a 1-3 mm layer on top of peat (Pro-Mix®PGX). Additionally, 40 trays were filled only with peat to examine seed contamination in the substrate, then all germination trays were randomly placed in a greenhouse and maintained under natural conditions (approximately under a 12 h- photoperiod and a mean temperature of 3.5 °C at night, and 22.8 °C during the day). Following Basto *et al*. (2018), trays were watered daily from below with tap water, and seedling emergence was recorded weekly for one year and four months. Soon after emergence, seedlings were removed and identified to species level. Seedlings that were difficult to identify were planted in new pots, to promote growing and flowering, to make identification easier. Seedling identification was strenuous because of the lack of seedling taxonomic determination guides and seedling reference collections of the high montane forest species of Colombia. Photographs of some high Andean forest seedlings were used as a guide (see Borda & Vargas, 2011). Moreover, this seed bank study was supported by seedling field observation and the vegetation survey, which facilitated seedling identification. The vegetation survey was also used to differentiate the possible type of seed bank of each species recorded in the soils. Our approach followed the dichotomous key proposed by Thompson *et al*. (1997) to assign every single species to transient, short-term persistent, or long-term persistent seed bank types.

Vegetation and litter cover sampling and characterization

Data were collected between July and August 2014. As described by Tulande-M. *et al*. (2018b), the vegetation was measured via the line-intercept method. Five parallel transects of 10 m each and 2 m apart were established inside each plot (10 x 10 m). Each transect was divided into 10 regular intervals of 1 m. The length covered by each species was measured with a tape located on each transect. The length of a transect was used to calculate the cover of the species. We also measured litter cover, in each transect, in the same way as vegetation cover (n = 450 measurements/area; n = 2 250 total). We define plant litter for the high Andean forest as leaf litter and, for the plantation and the areas where exotic species had been clearcut at different times, as needle litter and wood residues of small size lying loose on the soil.

Statistical analyses

The response variables for the seed bank data were the total number of seeds, the number of species, and the number of seeds of the ten most abundant species. Generalized Linear Mixed Models (GLMMs) were fitted using the R-package lme4 (Bates *et al*., 2013; R Core Team, 2018). All models were fitted with soil pH, litter cover, and sample depth as fixed effects, plus area (i.e., the high Andean forest, plantation, 0-8 months, 2.5 and 4.5 years of clearcutting) as a random effect with Poisson error distributions. Following Millar & Anderson (2004), we used both fixed and random effects due to the lack of independence in the data. To interpret random effect intercepts we used the ranef function in the lme4 package in R (Bates *et al*., 2013; R Core Team, 2018). To compare the species and life-form composition among areas, we performed analyses of similarities (ANOSIM) employing a Bray-Curtis distance measure. The anosim function in the vegan package in R was used for the analyses (R Core Team, 2018; Oksanen *et al*., 2019). Species and life-form diversity were assessed by using Shannon-Waver index. These analyses were carried out in R, using the vegan package (R Core Team, 2018; Oksane *et al*. 2019).

To test whether aboveground cover affected the mean number of seeds of the ten most abundant species recorded in the soils, Generalized Linear Models (GLM) were fitted with aboveground mean abundance and area with quasi-Poisson error distributions. All statistical analyses were conducted in R (R Core Team, 2018). The aboveground and seed bank communities were compared using an analysis of similarities (ANOSIM) and a Bray-Curtis distance measure. The anosim function in the vegan package in R was used for these analyses (R Core Team, 2018; Oksanen *et al*., 2019).

To prevent differences in sampling scales, vegetation data were transformed to relative cover and seed bank data to relative abundance and then analysed (Basto *et al.*, 2018).

Results

Seed bank abundance, richness, and composition

A total of 4 440 seedlings emerged from the seed banks of all study areas. These seedlings belong to 31 species, 30 genera, and 14 families (**Table 1**). Of these species, four were classified as transient, 18 as short-term persistent, and nine as long-term persistent (**Table 2**). The most abundant native species (with more than 30 seeds recorded in the soil) were *Carex pygmaea* (1 343 individuals), *Salvia* sp. (560), *Galium hypocarpium* (467), *Solanum americanum* (321), *Lachemilla fulvescens* (182), *Gnaphalium* sp. (132), *Hydrocotyle bonplandii* (87), *Agrostis perennans* (82), *Phytolacca bogotensis* (44), and *Stachys bogotensis* (43) (Table 1).

After clearcutting *P. patula* plantations, total seed bank abundance, richness, and seed bank size of the ten most abundant species increased in areas with 2.5 and 4.5 years after clearcutting (**Table 3**). However, we did not record any woody species in these areas, the only tree species recruited from seed banks was *Baccharis latifolia*, recorded and yet scarce (four seeds) in the high Andean forest (Table 1). A rising seed bank size in areas with 2.5 and 4.5 years after clearcutting was reflected by an increase in species and life-form diversity compared to the other assessed areas (Table 1). Moreover, the analysis of similarity showed that species and life-form composition were different among the studied areas (ANOSIM statistic R = 0.6, P = 0.001 and R = 0.5, P = 0.001, respectively). Only two herbs, *C. pygmaea* and *Oxalis corniculata*, were found in all study areas. However, when we compared the high Andean forest and the three areas with different post-clearcutting ages, nine herbs and one shrub were in common with the 0-8 month clear-cut area, and nine herbs were common to the forest and the areas of clear-cut ages 2.5 and 4.5 years (Table 1).

The number of seeds and species decreased significantly as soil sample depth increased (Generalized Linear Mixed Models; estimate ± s.e. of the estimate of the fixed effect parameter in the model = -0.04 ± 0.003; z-test = -14.1, $P < 0.00001$ and -0.03 ± 0.005; $z = -4.8$, $P < 0.00001$, respectively). Similarly, the abundance of the ten most abundant species decreased as soil sample depth increased (**Table 4**).

Table 1. Seed bank abundance and Shannon-Weiner diversity index recorded in areas after clearcutting *Pinus patula* plantations at Parque Forestal Embalse del Neusa, Colombia. Native species are identified with an asterisk. No information available is shown with a hyphen.

Family	**Species**	**Dispersal syndrome**	**Successional state**	**Native forest**	**Plantation**	**Time after the clearcutting**			**Total**
						0-8 months	**2.5 years**	**4.5 years**	
Herbs									
Araliaceae	*Hydrocotyle bonplandii**	Anemochory	Pioneer	0	0	3	74	10	**87**
Compositae	*Ageratina gracilis**	Anemochory	Pioneer	0	0	0	1	2	**3**
Compositae	*Conyza floribunda*	Anemochory	Pioneer	0	0	0	1	0	**1**
Compositae	*Gamochaeta americana**	Anemochory	Pioneer	6	0	1	18	5	**30**
Compositae	*Gnaphalium* sp.*	Anemochory	Pioneer	10	0	1	79	42	**132**
Compositae	*Hieracium avilae**	Anemochory	Pioneer	0	0	0	4	1	**5**
Compositae	*Hypochaeris radicata*	Anemochory	Pioneer	1	0	3	24	42	**70**
Compositae	*Sigesbeckia jorullensis**	Anemochory	-	0	0	1	0	0	**1**
Compositae	*Taraxacum officinale*	Anemochory	Pioneer	0	0	0	4	0	**4**
Cyperaceae	*Carex luridiformis**	Anemochory	-	0	0	0	1	3	**4**
Cyperaceae	*Carex pygmaea**	Anemochory	-	44	63	25	626	585	**1343**
Cyperaceae	*Cyperus aggregatus*	Anemochory	-	3	0	3	3	3	**12**
Lamiaceae	*Salvia* sp.*	Unassisted	-	0	0	9	266	285	**560**
Lamiaceae	*Stachys bogotensis**	Unassisted	-	0	0	9	12	22	**43**
Leguminosae	*Trifolium repens*	Anemochory/ zoochory	Pioneer	0	0	2	8	2	**12**
Oxalidaceae	*Oxalis corniculata*	Zoochory	Pioneer	7	3	5	29	17	**61**
Phytolaccaceae	*Phytolacca bogotensis**	Zoochory	Pioneer	0	0	2	23	19	**44**
Plantaginaceae	*Digitalis purpurea*	Anemochory	-	0	0	4	219	454	**677**
Polygonaceae	*Polygonum nepalense*	Zoochory	Pioneer	0	0	0	1	0	**1**
Polygonaceae	*Rumex acetosella*	Anemochory/ hydrochory	Pioneer	1	0	14	59	69	**143**
Rosaceae	*Lachemilla fulvescens**	Anemochory	Pioneer	0	0	4	96	82	**182**
Rubiaceae	*Galium hypocarpium**	Zoochory	Pioneer	2	0	53	312	100	**467**
Solanaceae	*Solanum americanum**	Zoochory	Pioneer	2	0	11	205	103	**321**
Grasses									
Poaceae	*Agrostis perennans**	Anemochory	-	0	0	2	39	41	**82**
Poaceae	*Anthoxanthum odoratum*	Anemochory	-	0	0	0	10	8	**18**
Poaceae	*Holcus lanatus*	Anemochory/ hydrochory	-	0	0	0	31	61	**92**
Poaceae	*Pennisetum clandestinum*	Anemochory/ hydrochory	-	0	0	0	8	1	**9**
Poaceae	*Stipa* sp.	Anemochory	Pioneer	0	4	12	7	1	**24**
Shrubs									
Hypericaceae	*Hypericum juniperinum**	Anemochory	Pioneer	0	0	0	1	0	**1**
Rosaceae	*Rubus floribundus**	Zoochory	Pioneer	2	0	5	0	0	**7**
Trees									
Compositae	*Baccharis latifolia**	Anemochory	Pioneer	4	0	0	0	0	**4**
Total number of seeds				**82**	**70**	**169**	**2161**	**1958**	**4440**
Shannon-Weiner diversity index (species diversity)				3.8	1.7	5.9	13.9	13.7	
Shannon-Weiner diversity index (life-form diversity)				1.3	1.1	2.2	3.0	3.0	

Table 2. Species occurring in aboveground vegetation and seed banks in areas after clearcutting *Pinus patula* plantations at Parque Forestal Embalse del Neusa, and their seed bank type. Following Thompson *et al.* (1997), three seed bank types were identified: transient (T), short-term persistent (ST-P), and long-term persistent (LT-P). Species registered as long-term persistent in the database of Thompson *et al.* (1997) are indicated with an asterisk. The presence of each species in the vegetation aboveground (Veg) is marked by an X. The number of seeds in the upper (Up) and lower (Low) soil layers is shown, which indicates its presence in the seed bank. Empty cells indicate the absence of species in the vegetation or in the seed bank.

Family	**Species**	**Habit**	**Seed bank type**	**Native forest**			**Plantation**			**0-8 months after clearcutting**			**2.5 years after clearcutting**			**4.5 years after clearcutting**		
				Veg	**Up**	**Low**	**Veg**	**Up**	**Low**	**Veg**	**Up**	**Low**	**Veg**	**Up**	**Low**	**Veg**	**Up**	**Low**
Adoxaceae	*Viburnum triphyllum*	Tree	T	X									X			X		
Alstroemeriaceae	*Bomarea* sp.	Herb	T	X														
Araliaceae	*Hydrocotyle bonplandii*	Herb	ST-P									3	X	48	26	X	6	4
Betulaceae	*Alnus acuminata*	Tree	T										X			X		
Bromeliaceae	*Bromelia* sp.	Herb	T	X														
Caryophyllaceae	*Cerastium arvense**	Herb	T										X			X		
Clethraceae	*Clethra fimbriata*	Tree	T	X														
Clusiaceae	*Clusia multiflora*	Tree	T	X														
Compositae	*Ageratina gracilis*	Herb	ST-P										X		1	X	2	
Compositae	*Baccharis bogotensis*	Tree	T										X			X		
Compositae	*Baccharis latifolia*	Tree	LT-P		2	2										X		
Compositae	*Bidens triplinervia*	Herb	T										X					
Compositae	*Conyza floribunda*	Herb	T										X	1				
Compositae	*Gamochaeta americana*	Herb	ST-P		3	3					1			11	7		3	2
Compositae	*Gnaphalium* sp.	Herb	ST-P		4	6						1	X	64	15	X	21	21
Compositae	*Hieracium avilae*	Herb	LT-P										X	1	3		1	
Compositae	*Hypochaeris radicata**	Herb	ST-P			1				X	1	2	X	13	11	X	27	15
Compositae	*Munnozia cf. senecionidis*	Herb	T	X														
Compositae	*Sigesbeckia jorullensis*	Herb	T							X	1							
Compositae	*Taraxacum officinale**	Herb	ST-P											3	1	X		
Cunoniaceae	*Weinmannia tomentosa*	Tree	T	X						X								

Cyperaceae	*Carex luridiformis*	Herb	LT-P												1		1	2
Cyperaceae	*Carex pygmaea*	Herb	LT-P		26	18		41	22	X	10	15	X	345	281	X	325	260
Cyperaceae	*Cyperus aggregatus*	Herb	LT-P		1	2					1	2	X		3	X	3	
Elaeocarpaceae	*Vallea stipularis*	Tree	T	X									X					
Geraniaceae	*Geranium sibbaldioides*	Herb	T													X		
Hypericaceae	*Hypericum juniperinum*	Shrub	T											1				
Lamiaceae	*Salvia* sp.	Herb	ST-P							X	4	5	X	232	34	X	231	54
Lamiaceae	*Stachys bogotensis*	Herb	ST-P								4	5		12		X	22	
Lauraceae	*Persea* sp.	Tree	T	X														
Leguminosae	*Trifolium repens**	Herb	ST-P									2	X	6	2	X	1	1
Melastomataceae	*Bucquetia glutinosa*	Tree	T	X														
Melastomataceae	*Miconia* sp. *1*	Tree	T	X														
Melastomataceae	*Miconia* sp. *2*	Tree	T										X					
Melastomataceae	*Miconia theaezans*	Tree	T	X														
Myricaceae	*Morella pubescens*	Tree	T													X		
Myrsinaceae	*Citharexylum* sp.	Tree	T	X														
Orchidaceae	*Elleanthus* sp.	Herb	T	X														
Oxalidaceae	*Oxalis corniculata**	Herb	ST-P		4	3		2	1		4	1	X	16	13	X	9	8
Phytolaccaceae	*Phytolacca bogotensis*	Herb	LT-P							X		2	X	7	16		10	9
Pinaceae	*Pinus patula*	Tree	T				X			X			X			X		
Piperaceae	*Peperomia microphylla*	Herb	T										X					
Plantaginaceae	*Digitalis purpurea**	Herb	LT-P									4	X	91	128	X	186	268
Plantaginaceae	*Veronica serpyllifolia**	Herb	T													X		
Poaceae	*Agrostis perennans*	Grass	ST-P									2		29	10	X	30	11
Poaceae	*Anthoxanthum odoratum**	Grass	LT-P										X	7	3	X	5	3
Poaceae	*Calamagrostis* sp.	Grass	T													X		
Poaceae	*Chusquea scandens*	Shrub	T	X														
Poaceae	*Holcus lanatus**	Grass	ST-P										X	18	13	X	46	15
Poaceae	*Pennisetum clandestinum*	Grass	T										X	8		X	1	
Poaceae	*Stipa* sp.	Grass	ST-P					4			4	8		6	1	X	1	
Polygonaceae	*Muehlenbeckia tamnifolia*	Shrub	T							X			X			X		
Polygonaceae	*Polygonum nepalense*	Herb	LT-P												1			

Polygonaceae	*Rumex acetosella**	Herb	ST-P		1							14	X	36	23	X	51	18
Primulaceae	*Myrsine coriacea*	Tree	T	X														
Rosaceae	*Hesperomeles goudotiana*	Tree	T													X		
Rosaceae	*Lachemilla fulvescens*	Herb	ST-P								1	3	X	62	34	X	57	25
Rosaceae	*Rubus bogotensis*	Shrub	T										X			X		
Rosaceae	*Rubus floribundus*	Shrub	ST-P		2						3	2	X			X		
Rosaceae	*Rubus glaucus*	Shrub	T										X					
Rubiaceae	*Galium hypocarpium*	Herb	ST-P		1	1					29	24	X	196	116	X	65	35
Rubiaceae	*Nertera granadensis*	Herb	T										X					
Rubiaceae	*Palicourea* sp.	Shrub	T	X														
Solanaceae	*Brugmansia sanguinea*	Shrub	T										X					
Solanaceae	*Salpichroa tristis*	Herb	T										X			X		
Solanaceae	*Solanum americanum*	Herb	ST-P		1	1				X	7	4	X	147	58		68	35
Winteraceae	*Drimys granadensis*	Tree	T	X														

Effect of the aboveground vegetation on seed banks

Most of the aboveground species were not represented in the seed bank. We recorded 63 species in the vegetation of which 38.1 % were represented in seed banks (Table 2); our analysis of similarities showed that seed bank and aboveground plant community species compositions differed (ANOSIM statistic $R = 0.53$; $P = 0.001$). Furthermore, the aboveground vegetation did have a lot of woody representatives while only one species was recorded in the soils (Table 2). Species present in the vegetation aboveground but absent in the soil were classified as transient (Table 2).

Despite the low similarity between vegetation and seed banks, the results of examining the effect of the vegetation cover on the seed bank size showed that most species-specific responses reflected those aboveground; i.e. increases in vegetation cover led to a significant increase in the mean number of seeds for seven of the ten most abundant species in the study (**Table 5**).

Effect of soil pH on seed banks

After clearcutting pine plantations, we detected an increase in soil pH leading to a significant change in seed bank abundance and richness. Specifically, we

Table 3. Random effect on seed bank abundance, richness, and size of the ten most abundant species, in areas after clearcutting *Pinus patula* plantations at the Parque Forestal Embalse del Neusa, Colombia. The intercept for each study area is shown. Positive values = an increase in the total number of seeds, the number of species and the number of seeds of the ten most abundant species and negative values = a decrease in these response variables.

Seed bank response variables	Plantation	0-8 months	2.5 years	4.5 years	Forest
Total seed bank abundance	-1.6	-0.4	1.5	1.4	-0.9
Species richness	-1.1	-0.2	1.2	1.03	-0.9
Carex pygmaea	-0.8	-1.6	1.6	1.6	-0.9
Digitalis purpurea	-2.7	0.4	3.1	3.7	-2.4
Salvia sp.	-2.9	0.8	3.3	3.3	-2.5
Galium hypocarpium	-3.2	1.8	2.3	1.0	-1.2
Solanum americanum	-3.3	-0.1	3.2	2.6	-1.6
Lachemilla fulvescens	-2.3	0.7	2.1	2.0	-1.4
Rumex acetosella	-3.1	0.9	1.8	2.2	-1.1
Gnaphalium sp.	-2.6	-1.6	2.5	2.0	0.6
Holcus lanatus	-1.2	-0.8	5.2	6.1	-0.5
Hydrocotyle bonplandii	-1.5	0.6	2.9	0.7	-1.6

recorded the highest number of seeds (3 086) within a soil pH range from 4.65 to 5.2 (GLMM; 0.96 ± 0.06; $z = 17.3$, $P < 0.00001$) and the richest seed banks (10-13 species) at soil pH 4.63 to 5.05 (GLMM; 0.58 ± 0.1; $z = 6$, $P < 0.00001$). Some species showed a significant increase in the number of seeds under specific soil pH (Table 4). In particular, seed banks of *C. pygmaea* at pH = 4.4-5.04, *D. purpurea* at pH = 4.65-5.19, *Salvia* sp. at pH = 4.96-5.19, *G. hypocarpium* at pH = 4.69-5.2, *L. fulvescens* at pH = 4.83-5.05, and *H. lanatus* at pH = 4.75-5.19 (**Fig. 2**).

The effect of litter cover on seed banks

Increases in litter cover led to a significant decrease in total seed bank abundance (GLMM; -0.12 ± 0.03; $z = -4.03$, $P < 0.00001$), species richness

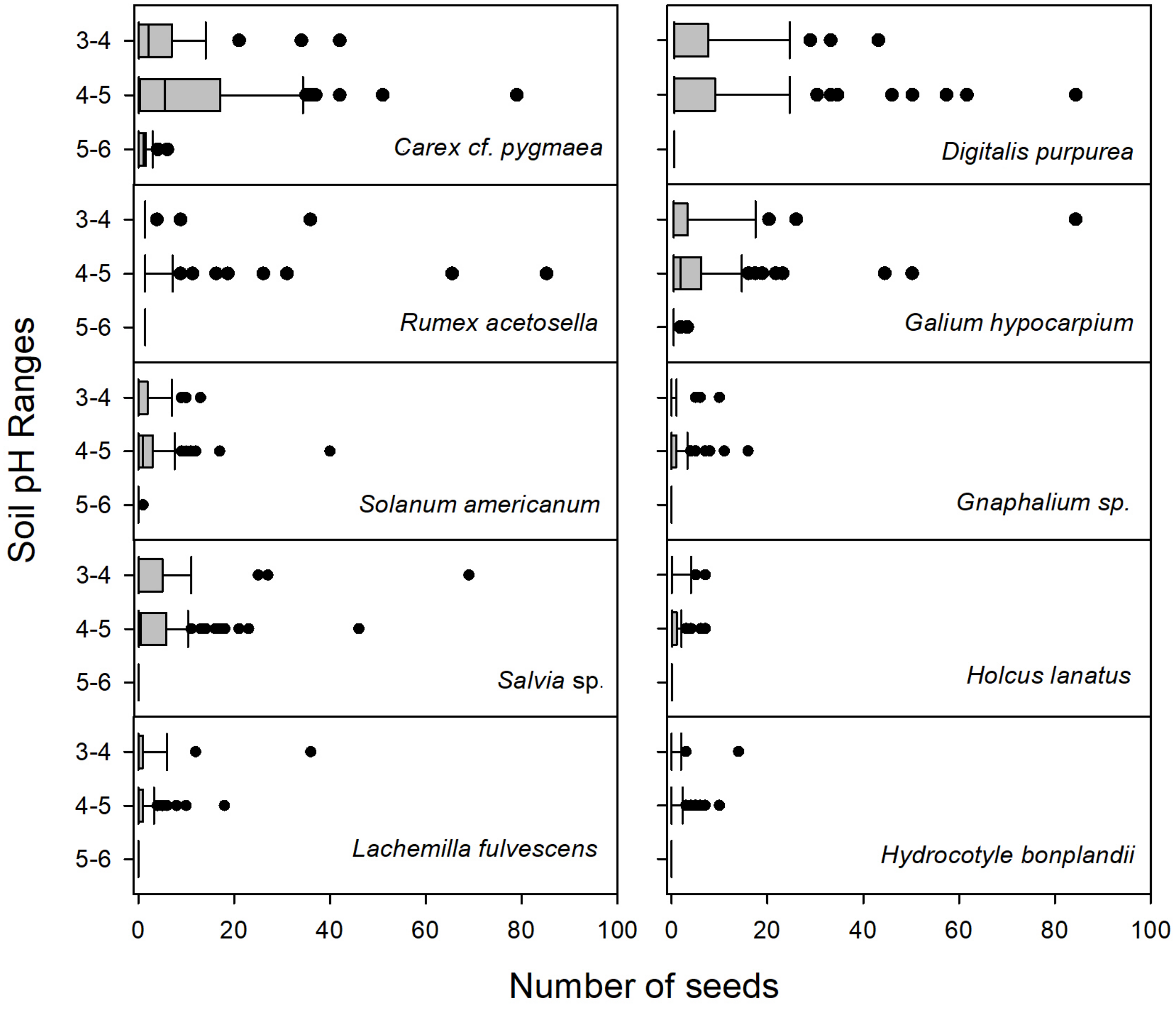

Figure 2. Effect of soil pH on the number of seeds of the ten most abundant species germinating from seed banks in Parque Forestal Embalse del Neusa, Colombia, after clearcutting *Pinus patula* plantations.

(GLMM; -0.18 ± 0.05; $z = -3.6$, $P < 0.001$), and the number of seeds of *G. hypocarpium*, *L. fulvescens*, *R. acetosella*, and *H. bonplandii* (Table 4). Moreover, we recorded a significant decline in the abundance of *Salvia* sp. in soils with large litter cover and low pH (<4.13). While decreases in litter cover led to a significant increase in *C. pygmaea*, *D. purpurea*, *Salvia* sp., and *S. americanum* seed bank size (Table 4).

Table 4. Results of generalized linear mixed models (GLMMs) examining the effect of sample depth, soil pH, and litter cover on the seed bank size of the ten most abundant species in areas after clearcutting *Pinus patula* plantations within Parque Forestal Embalse del Neusa, Colombia. A significant factor is marked in bold font.

Species	Fixed effects in the models	Estimate	Standard error	*z* value	*P*
Carex pygmaea	Depth of the sample	-0.02	± 0.01	-4.1	**< 0.00001**
	Soil pH	0.25	± 0.1	2.4	**0.02**
	Litter cover	0.2	± 0.05	3.1	**0.01**
Digitalis purpurea	Depth of the sample	0.04	± 0.01	4.7	**< 0.00001**
	Soil pH	1.36	± 0.15	9.1	**< 0.00001**
	Litter cover	0.55	± 0.1	-6.5	**< 0.00001**
Salvia sp.	Depth of the sample	-0.16	± 0.01	-14.2	**< 0.00001**
	Soil pH	2.45	± 0.24	10.05	**< 0.00001**
	Litter cover	3.25	± 1.4	2.35	**0.02**
	Soil pH* litter cover	-0.74	±0.28	-2.61	**< 0.01**
Galium hypocarpium	Depth of the sample	-0.05	± 0.01	-5.3	**< 0.00001**
	Soil pH	1.64	± 0.2	10.4	**< 0.00001**
	Litter cover	-0.4	± 0.1	-4.2	**< 0.00001**
Solanum americanum	Depth of the sample	-0.1	± 0.01	-7	**< 0.00001**
	Soil pH	-0.06	± 0.2	-0.25	0.8
	Litter cover	0.3	± 0.1	3.3	**< 0.00001**
Lachemilla fulvescens	Depth of the sample	-0.07	± 0.02	-4.2	**< 0.00001**
	Soil pH	2.6	± 0.3	10.1	**< 0.0001**
	Litter cover	-0.4	± 0.15	-2.6	**0.01**
Rumex acetosella	Depth of the sample	-0.05	± 0.02	-2.8	**< 0.01**
	Soil pH	-0.25	± 0.6	-0.4	0.7
	Litter cover	-5.8	± 2.4	-2.4	**0.02**
Gnaphalium sp.	Depth of the sample	-0.07	± 0.02	-4.7	**< 0.00001**
	Soil pH	0.31	± 0.33	1	0.4
	Litter cover	0.2	± 0.15	1.1	0.3
Holcus lanatus	Depth of the sample	-0.08	± 0.03	-3.6	**< 0.001**
	Soil pH	2.02	± 0.4	5.2	**< 0.00001**
	Litter cover	0.2	± 0.2	1.14	0.3
Hydrocotyle bonplandii	Depth of the sample	-0.05	± 0.02	-2.2	**0.02**
	Soil pH	0.46	± 0.37	1.2	0.2
	Litter cover	-0.6	± 0.2	-3.02	**< 0.01**

Table 5. Results of a GLM examining the effect of mean vegetation cover on the mean number of seeds of the ten most abundant species recorded after clearcutting *Pinus patula* plantations in Andean high montane areas. A significant effect is highlighted in bold font; a positive Estimate (that is significant) indicates that the increases in vegetation cover of that species increased the number of seeds in the seed bank.

Species	Estimate	Standard error	*t* value	*P*
Carex pygmaea	-0.19	0.35	-0.55	0.58
Digitalis purpurea	3.76	1.08	3.50	**< 0.01**
Salvia sp.	2.02	0.86	2.40	**0.02**
Galium hypocarpium	3.29	0.60	5.46	**< 0.00001**
Solanum americanum	0.19	1.54	0.12	0.90
Lachemilla fulvescens	4.74	1.28	3.70	**< 0.001**
Rumex acetosella	2.96	1.39	2.13	**0.04**
Gnaphalium sp.	2.54	0.42	6.02	**< 0.00001**
Holcus lanatus	3.07	0.58	5.23	**< 0.00001**
Hydrocotyle bonplandii	2.48	1.71	1.45	0.15

Discussion

At PFEN, in the Colombian eastern Andes, the seed banks assessed responded to the clearcutting of *P. patula* plantations by increasing their total seed abundance, species richness, and the number of seeds of native and exotic species, as well as changing species composition. Moreover, we recorded an increase in species diversity which indicates that seed bank community structure is changing. Overall, seed bank responses were related to an increase in aboveground vegetation cover and soil pH and a decrease in litter cover. Broadly speaking, our results showed a similar trend to that recorded for other components of the ecosystem studied (Tulande-M. *et al*., 2018b).

The role of aboveground vegetation cover, soil pH, and litter cover on seed bank responses

Following the felling of pine plantations, the similarity between vegetation and seed banks was low; however, both native and exotic species seed abundance increased as aboveground vegetation augmented. This finding suggests that seed production is likely to have had an important role in seed bank changes after *P. patula* clearcutting. We based this affirmation on two facts: first, 61 % of the seeds were recorded at the soil surface layer (0-10 cm). Second, there was an increase in vegetation cover of exotic grasses and herbs, such as, *D. purpurea*, *R. acetosella*, and *H. lanatus* that led to an increase in the size of their seed banks. These species become established and rapidly increase in abundance after the clearcutting of *Pinus* sp. (Stanbury *et al*., 2018; Torres *et al*., 2018). In addition, seed banks were composed of a large number of wind-dispersed pioneer herbs and a small number of shrubs and tree species. A similar pattern was also recorded in the aboveground vegetation in our research and in other studies (Torres *et al*., 2018). Nevertheless, this could have been caused by seed dispersal of anemochorous species being facilitated by the removal of pines. Moreover, in 2014, there were changes in the rainfall pattern which might have reduced the number of shrubs and tree seeds in the soil. In particular, in June and July, the average precipitation was higher than the historical monthly average, while in August and September there was a rainfall deficit because the average precipitation was lower compared to the historical average (CAR, 2014).

Increased vegetation cover in areas after clearcutting of *Pinus* spp. modifies litter quality, which in turn increases soil pH (Stanbury *et al*., 2018). pH has been identified as one of the few soil abiotic conditions that changes after pine removal (Galloway *et al*., 2017). Evidence in temperate ecosystems suggests that pH has an effect on seed abundance and persistence in the soil (Pakeman *et al*., 2012; Basto *et al*., 2015). Our results show that increases in pH led to a greater seed bank abundance and richness in Andean high montane areas. Even though, our approach did not aim at identifying the causes that explain this finding, we consider that microbial activity might have influenced seed longevity at specific soil pH values, as has been suggested in previous studies (Basto *et al*., 2015).

The role of reducing litter cover on the increase in seed bank abundance and richness has a straightforward interpretation. The *Pinus* sp. needle layer acts as a selective barrier to the entry of seeds of some species to the soil (Bueno & Baruch, 2011; Egawa & Tsuyuzaki, 2013). Therefore, the depletion of the litter layer in our study area, after pine plantation removal, could have facilitated seed bank formation.

Recommendations for the ecological restoration of high montane forests

Monitoring changes occurring after clearcutting of pines makes it easier to choose the restoration strategy (Cuevas & Zalba, 2010), in particular, it is necessary to identify which native species have the capacity to recolonize the area by recruitment from seed banks (Cuevas & Zalba, 2010). The use of seed banks to restore degraded ecosystems is limited to the persistence of seeds in the soil, therefore, long-term persistent seed banks are the only ones that might contribute to aboveground vegetation recovery (Thompson *et al*., 1997). Our approach identified nine species as long-term persistent; this highlights their potential use to recruit these species from the soil seed bank. However, taking into account that our seed bank sampling was carried out at one particular time (by the end of the dry season in 2014), we rise the caveat that the classification of seed bank types proposed here could change by incorporating data from other seasons.

Nevertheless, our overall findings indicate that the seed bank contributes only to the reestablishment of some herbaceous plants after pine tree clearcutting. These results agree with conclusions of experiments of thinning exotic species in high Andean areas (Corredor & Vargas, 2007; León & Vargas, 2007). In addition, we recorded that the seed bank sizes of shrubs and trees were too small, which may constrain the natural regeneration processes and therefore the restoration of the high montane forests. Furthermore, seed banks from soils of the pine plantation were too poor to contribute to the natural regeneration process, which also supports previous findings (León & Vargas, 2007; Borda & Vargas, 2011).

Our results support the conclusion that recruitment from the seed bank is not sufficient for recovering native vegetation in areas previously covered with pine tree plantations (Rago *et al*., 2020). Consequently, active restoration strategies should be applied in these areas (Cuevas & Zalba, 2010; Galloway *et al*., 2017). First, actions promoting native vegetation reestablishment should be applied (Rago *et al*., 2020), namely via direct seeding or planting (Galloway *et al*., 2017) or seed dispersal processes from native adjacent areas (Jadán *et al*., 2019). Furthermore, a vegetation management plan should be executed to boost seed production (e.g. protecting floral parts from grazing) to increase seed bank size and its potential for vegetation recovery (Mndela *et al*., 2020). Second, previous studies suggest removing the litter layer to improve restoration via seed banks (Bueno & Baruch, 2011 but see León & Vargas, 2007); our results support this recommendation. Finally, we suggest examining the soil pH before evaluating the potential use of seed banks to recover the native vegetation. pH influences other soil characteristics and processes (chemical, physical, and biological) (Neina, 2019). Our study shows that the seed bank improved as soil pH increased. Therefore, manipulating soil pH might increase the speed of the restoration process (Prach *et al*. 2007) as well as seed bank recovery. Increasing, in turn, their potential to recruit some species from seeds in the soils.

Conclusions

Overall, our results show that in high Andean areas, after the removal of *Pinus patula* plantations, seed bank responses mostly reflect changes occurring in the current aboveground vegetation, litter cover, and soil pH. Specifically, seed bank features improved with the increase of aboveground vegetation cover and soil pH and the decrease of litter cover. However, the seed bank's role in the recovery of native plants is limited to some herbaceous species, which indicates that there is a need for active restoration.

This research shows that seed bank knowledge is an important tool to inform decisions about the restoration of high montane forests, specifically: 1) to identify the barriers that limit regeneration processes; and 2) to decide which kind of ecological restoration strategy should be implemented.

We are aware that the short period after pine plantation clearcutting (0-4.5 years) offers a limited time span to identify the responses of the seed banks assessed. We thus recommend our conclusions to be interpreted with caution.

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Conflict of interest

The authors declare that there are no conflicts of interest.

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Respuestas del banco de semillas después de la tala rasa de plantaciones de *Pinus patula* en áreas de alta montaña andina

Resumen: La tala rasa de plantaciones exóticas favorece los procesos de regeneración natural, en los que el banco de semillas puede jugar un papel importante. En áreas de alta montaña andina, después de la tala rasa de *Pinus patula*, los cambios en el pH del suelo y la hojarasca conducen a un incremento en la biodiversidad de fauna y flora. Sin embargo, el impacto de estos cambios en el banco de semillas no se conoce todavía. El objetivo del presente estudio fue entender cómo cambia la riqueza, abundancia y composición del banco de semillas después de la tala rasa de *P. patula*, e identificar el papel de la cobertura de la vegetación en pie, el pH y la cobertura de hojarasca en estas variaciones del banco de semillas. El estudio se llevó a cabo en tres áreas con diferentes edades post-tala (0, 2.5, 4.5 años), una plantación de *P. patula* y un parche de bosque altoandino. Todos estos sitios se localizaron entre 3033 y 3100 m.s.n.m. La abundancia del banco de semillas, la riqueza, y el número de semillas de las diez especies más abundantes aumentaron en áreas con 2.5 y 4.5 años después de la tala. Además, la composición del banco de semillas fue diferente entre las áreas estudiadas. Estos cambios se relacionaron con el aumento de la cobertura de la vegetación en pie, el pH del suelo y la reducción de la cobertura de hojarasca. Los bancos de semillas contribuyeron casi exclusivamente a la recuperación de algunas especies herbáceas; se registró únicamente una especie arbórea colectada de los bancos de semillas (*Baccharis latifolia*) en los suelos del bosque; por tanto, los procesos de regeneración natural pueden estar limitados. Nuestros estudios resaltan la necesidad de implementar restauración activa para acelerar la recuperación de bosque alto andino en áreas previamente coberturas con plantaciones de pino.

Palabras clave: tala rasa; hojarasca de pino; *Pinus* sp.; sucesión secundaria; pH del suelo.

Resposta do banco de sementes depois de um corta raso de plantações de *Pinus patula* em áreas de alta montanha andina

Resumo: O corte raso de plantações exóticas favorece os processos de regeneração natural, no qual o banco de sementes pode ter um papel importante. Em áreas de alta montanha andina, depois do corte raso de *Pinus patula*, as alterações do pH do solo e a serrapilheira conduzem a um aumento na biodiversidade de fauna e flora. Entretanto, o impacto destas mudanças no banco de sementes ainda não é conhecido. O objetivo do presente estudo foi entender como a riqueza, abundância e composição do banco de sementes é modificada depois de um corta raso de *P. patula*, e identificar o papel da cobertura da vegetação em pé, o pH e a cobertura serrapilheira nestas variações do banco de sementes. O estudo se realizou em três áreas com diferentes idades pós-corte (0, 2.5, 4.5 anos), uma plantação de *P. patula* e um trecho de bosque alto-andino. Todas estas áreas se localizaram entre 3033 e 3100 metros de altura. A abundância do banco de sementes, a riqueza, e o número de sementes das dez espécies mais abundantes aumentaram em áreas com 2.5 e 4.5 anos depois do corte. Além disso, a composição do banco de sementes foi diferente entre as áreas estudadas. Estas mudanças se relacionaram com o aumento da cobertura de vegetação em pé, o pH do solo e a redução da cobertura serrapilheira. Os bancos de sementes contribuíram quase exclusivamente a recuperação de algumas espécies herbais; registrou-se apenas uma espécie de árvore coletada dos bancos de sementes (*Baccharis latifolia*) nos solos do bosque; motivo pelo qual os processos de regeneração natural podem estar constrangidos. Nossos estudos ressaltam a necessidade de implementar restauração ativa para acelerar a recuperação de bosque alto andino em áreas previamente cobertas com plantações de pinho.

Palavras-chave: corte raso; serrapilheira de pinho; *Pinus* sp; sucessão secundaria; pH do solo.

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