Ecological Management & Restoration

ARTICLE

Lessons Learned From Direct Seeding to Restore Degraded Mountains in Cauca, Colombia

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Received: 12 March 2024 | **Revised:** 24 October 2024 | **Accepted:** 11 December 2024

Funding: This work was supported by PUR Projet.

Keywords: degraded landscapes | forest recovery | restoration costs | seed germination

ABSTRACT

Direct seeding is a technique frequently used to restore degraded lands worldwide. Direct seeding is attractive to restore degraded lands mainly because of its low cost compared to planting seedlings. However, this technique has been poorly studied in tropical mountains. Here, we investigated the outcomes of direct seeding at four degraded sites in the Andean mountains of Cauca, Colombia. We used 45 native tree species, most of them commonly used in restoration projects in the Andean region of Colombia. After 150 days of sowing, we evaluated seedling emergence, survival and establishment costs. Performance of direct seeding was markedly different across sites. Most species had low seedling emergence, with Guayaba (*Psidium guajava*) and Matachande (*Bocconia frutescens*) showing the highest emergence. Species with large seeds showed higher emergence compared with medium and small seeds. Seedling density was considerably variable among sites, ranging from 496 to 5550 ind. ha^{-1}. Our results evidence the need for long-term monitoring at mountain restoration sites and that restoring tropical degraded mountains using direct seeding is a challenge that can be complemented with native tree planting. Further research is required to explore the advantages and disadvantages of direct seeding in mountain terrain.

1 | Introduction

Tropical mountain ecosystems are at the heart of the United Nations (UN) Decade on Ecosystem Restoration. Recently, the UN General Assembly declared 2022 as the International Year of Sustainable Mountain Development (United Nations 2021). A key result of this year was the declaration of 2023–2027 as 'Five Years of Action for the Development of Mountain Regions' (Mountain Partnership Secretariat 2022). Tropical mountains worldwide provide ecosystem services to people and society, such as carbon sequestration, water regulation and supply, timber and food provision, erosion control and cultural services (Costanza et al. 1997; Dimitrov, Nogués-Bravo, and Scharff 2012; Mengist, Soromessa, and Legese 2020). Despite their importance, most tropical mountain ecosystems are severely degraded due to land conversion for agriculture, pasture and commercial tree monocultures; invasion by exotic animals and plants; and accelerating climate change impacts (Christmann and Menor 2021).

Ecosystem restoration in mountains has become a major task worldwide, helping to recover and reverse lost biodiversity and ecosystem functioning and improve local livelihoods (Chazdon et al. 2017; Brancalion et al. 2019; Di Sacco et al. 2021). The most common strategy to restore degraded tropical mountains is to

Summary

- Implications for managers
  - Direct seeding in tropical mountains requires careful timing with the rainy season and minimising soil disturbance to prevent erosion. Mountain landscapes can be sensitive, and soil erosion must be avoided during site preparation.
  - Forest species selection is key for direct seeding performance. It is important to work with high-quality seeds and to understand the species response under different mountain soil conditions.
  - In tropical mountains, direct seeding requires extensive weed control during the first months to ensure better native seedling survival and growth rates.

plant nursery-grown tree seedlings (Cole et al. 2011; Atondo-Bueno, Bonilla-Moheno, and López-Barrera 2018). However, securing seedlings for tree planting has been difficult due to high nursery costs and high labour efforts associated with planting (i.e., seedling transportation, soil preparation, mechanical weed control or fertiliser application) (Ceccon, González, and Martorell 2016).

There is also low availability and diversity of species in nurseries (Cole et al. 2011). A cost-effective alternative to using seedlings is direct seeding. Direct seeding involves the collection of seeds from mother trees around the restoration area and directly sowing them at the restoration site (Atondo-Bueno et al. 2016). In recent years, direct seeding has been considered an attractive strategy to restore degraded lands due to its low cost and labor inputs as compared to planting seedlings (Ceccon, González, and Martorell 2016; Meli et al. 2018). With direct seeding, seeds can often be more cost-effective compared to growing seedlings, as the latter requires significant time and infrastructure. However, while seeds are often readily available near the restoration site, these same seeds could also be used to grow seedlings for planting (Shaw et al. 2020). In addition to being economical, direct seeding strengthens community engagement, as locals can support with species identification and seed collection (Atondo-Bueno et al. 2016). Direct seeding also comes with many ecological benefits, including a strong root network, high plant density and enhanced biodiversity. It is also a practical option for restoring large-scale sites (Piotrowski et al. 2023). However, it also presents several challenges. One significant limitation is the potential need for mechanised application to scale the method efficiently, particularly in extensive areas (Campos-Filho et al. 2013). Additionally, direct seeding often requires a higher quantity of seeds compared to planting seedlings because of potentially lower germination, survival and growth rates (Durigan, Guerin, and Da Costa 2013).

In South America, direct seeding has been commonly implemented in Brazil to restore lowland tropical forests or savanna woodlands (Engel and Parrotta 2001; Campos-Filho et al. 2013; Meli et al. 2018; Piotrowski et al. 2023). A recent systematic review by Lázaro-González et al. (2023) showed that most of the direct seeding studies focus on temperate and low-land regions. As for tropical mountain ecosystems, there are a limited number of studies on the efficacy of direct seeding (Bonilla-Moheno and Holl 2010). To the best of our knowledge, no studies have investigated the results of direct seeding to restore degraded mountain ecosystems of Colombia.

This paper investigates the technical, economic and ecological feasibility of direct seeding to restore degraded tropical mountains in Cauca, Colombia. For this case study, a high number of tree species were used for restoration. Specifically, 45 forest species were sowed at four degraded sites characterised by different levels of soil degradation, ranging from severe deterioration due to deforestation, intensive agriculture and grazing, to moderate degradation from sporadic agriculture and mixed vegetation cover over the past decades. We attempted to answer the following questions: (a) Is direct seeding an effective strategy to establish a high seedling density in tropical mountains? (b) How do the native species sown differ in their field performance (i.e., emergence and survival)? (c) Do seed size, dispersion syndrome and ecological group affect seed emergence?

2 | Methods

2.1 | Study Site

We conducted this study in the municipalities of Popayán and Cajibio, located in the Cauca department, Colombia (Figure 1). The climate is classified as tropical wet-dry with a historical mean annual precipitation of 2000 mm and a mean annual temperature of 21°C. The vegetation plots were established over areas previously covered by humid premontane forest (Solórzano et al. 2014). All sites are characterised by a high degree of geologic and topographic variability. Thus, the soils are variable, ranging from fertile Andisols to nutrient-poor Ultisols.

The sites were generally dominated by non-native trees or grass species and characterised by a low potential for natural regeneration, representing different levels of soil degradation, ranging from severe to moderate soil degradation (Figure 2). The degradation gradient was defined based on the restoration diagnostic conducted at each site (Rodrigues et al. 2011). Site 1 (2°29′50.95″ N, 76°43′30.52″ W; area: 1.1 ha; elevation: 1720 m) with severe soil degradation was covered by the invasive bracken Helecho Marranero (*Pteridium aquilinum*) and had scattered trees of Pino (*Pinus patula*) before direct seeding. The site was deforested in the middle of the 20th century. After deforestation, the site was occupied by coffee crops and later pine plantations. In 2000, the site was abandoned due to soil degradation. Site 2 (2°36′52.05″ N, 76°43′36.12″ W; area: 1.1 ha; elevation: 1640 m) was cleared first in 1980 by slash and burn and then heavily grazed for more than 30 years. The soil is mainly clayey, and it was mainly covered by grass species with some isolated native tree species. Site 3 (2°39′41.69″ N, 76°44′40.29″ W; area: 1.2 ha; elevation: 1690 m) was covered by grass, bracken and few shrub species. Land use on this site during the last 30 years is mainly associated with extensive livestock farming and includes frequent burning for transitory crops. Site 2 and Site 3 had intermediate soil degradation. Site 4 (2°37′46.68″ N, 76°33′39.63″ W; area: 1.3 ha; elevation: 1804 m) with moderate soil degradation was the most heterogeneous in its initial plant cover with areas with grass species, bracken, maize crops or scattered *Eucalyptus*

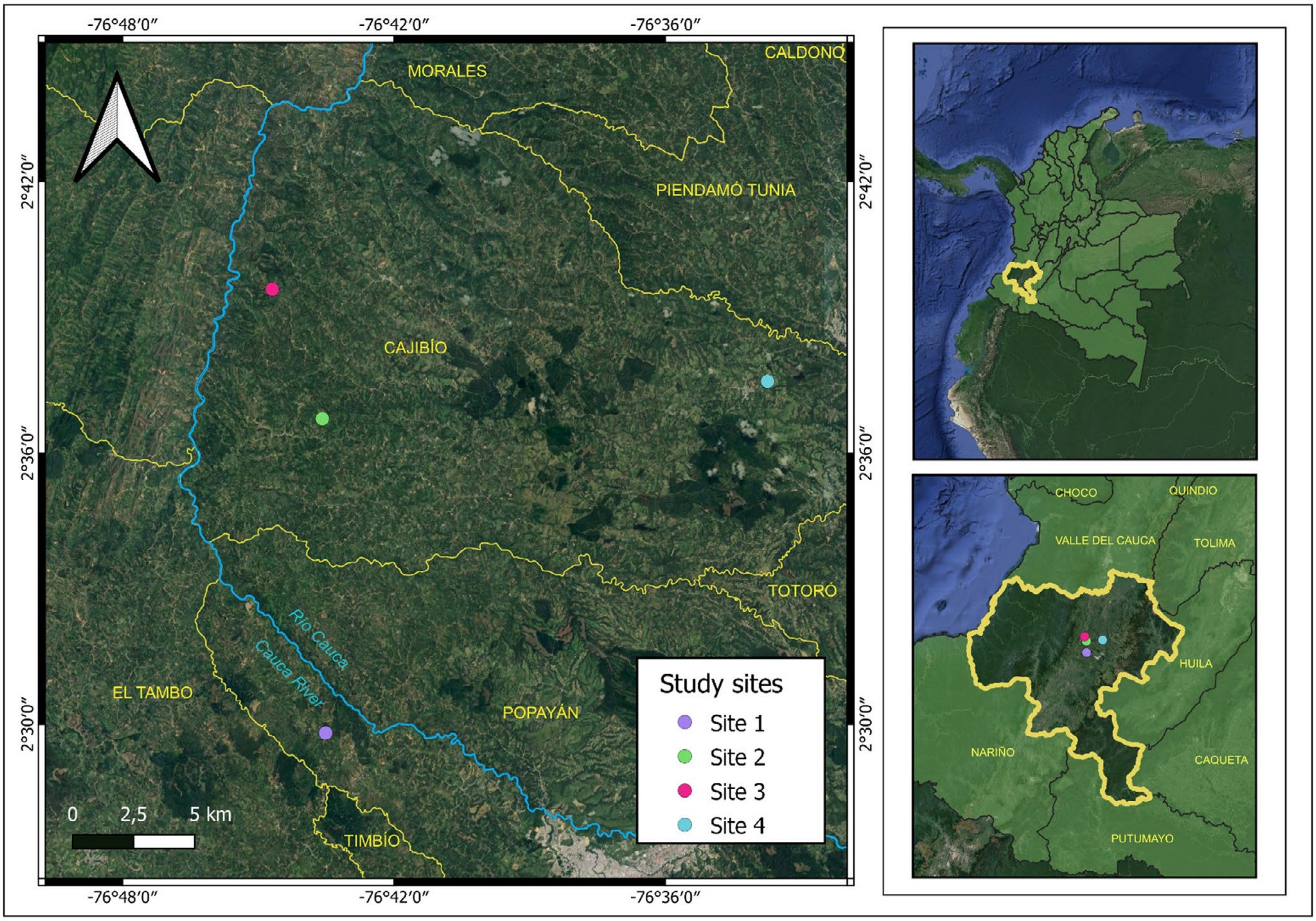

FIGURE 1 | Location of the four sites with direct seeding in the department of Cauca, Colombia, conducted between November and December 2022. The areas ranged from 1 to 1.3 ha, with a total of 45 species and 196.1 kg of seeds sown across all restoration sites.

trees. This site has been used sparingly for agriculture over the past 30 years.

2.2 | Species Selection

Species selection was primarily determined by seasonality and seed availability in the period prior to direct seeding. We used 45 native tree species distributed across 28 families and 44 genera. Most of these species (73%, 33 species) are commonly used in restoration projects in the Andean region of Colombia, especially in elevations between 1200 and 2200 m a.s.l. These tree species have diverse ecological attributes, a range of seed sizes, dispersal mechanisms and ecological groups (Table S1). Following similar investigations (Piotrowski et al. 2023), we grouped the seeds into three sizes: large, medium and small. Large seed group species have 1000 seeds per kg, medium class includes species with a quantity between 1000 and 10,000 seeds per kg and small seeds refer to species with more than 10,000 seeds per kg. The ecological group included pioneer and non-pioneer species based on information from the literature (Ceccon, González, and Martorell 2016; Souza and Engel 2018) and personal observations. Similarly, the dispersion syndrome was classified as anemochoric, autochoric and zoochoric. A total of 196.4 kg of seed (Table 1) was collected by 10 local farmers, who constituted the first network of seed collectors for forest restoration in Cauca.

2.3 | Steps for Direct Seeding

For soil preparation and management in the study sites, we followed the protocol proposed by Piotrowski, Silva, and Piña-Rodrigues (2020). Before seeding, it was necessary to reduce the competition of existing weeds in all sites. We used mechanical and chemical treatments during the clearing of each site. After clearing, we prepared the soil mechanically to reduce soil compaction and erosion, as well as improve the infiltration and break the surface crusts (Shaw et al. 2020). We used a tractor with mid-size offset disks for soil preparation. Due to the high level of soil degradation, we adjusted the soil nutrient status by applying lime ($CaCO_3$) after ploughing.

Direct seeding took place 2 days after soil preparation during the months of November and December 2022 in the middle of the rainy season. We used a mixture of native trees with annual legumes such as Frijol (*Phaseolus vulgaris*) and sub-perennial legumes, including Guandul (*Cajanus cajan*), regarded as green manure that will degrade into the soil after 4 years. Green manure plays an important role in the recovery process because it can help to improve soil quality, reduce the competition with exotic grasses and contribute to food security (Campos-Filho et al. 2013; Rodrigues et al. 2019). Total seeding density averaged for green manure was 60,000 seeds ha^{-1}, while tree seed density represented 250,000 seeds ha^{-1} (Piotrowski et al. 2023). All seeds were

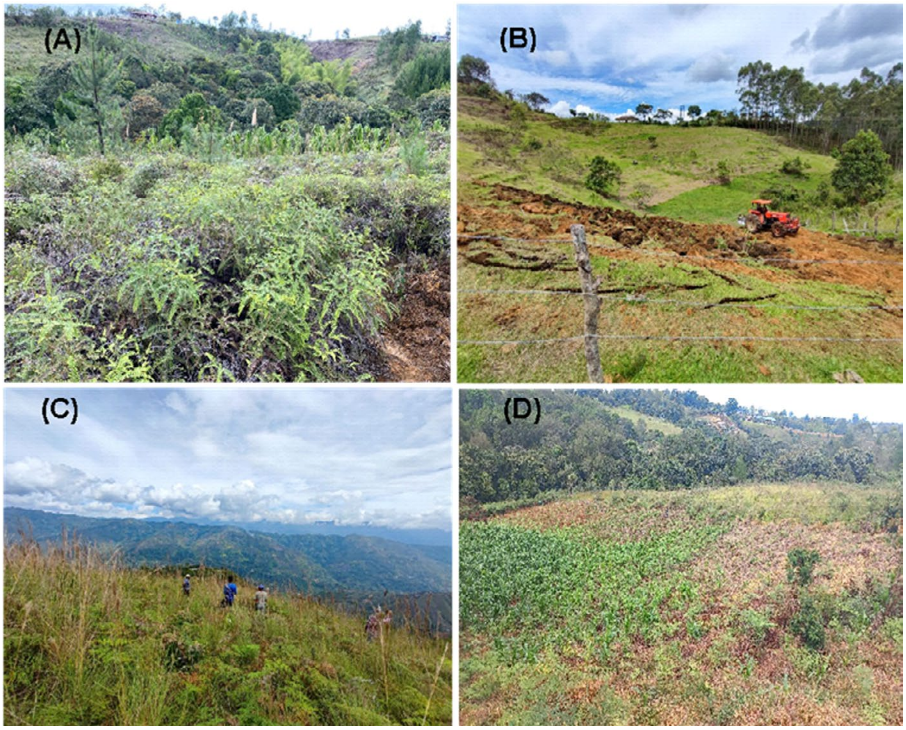

FIGURE 2 | Pictures showing the characteristic vegetation cover at each of the four sites (A: Site 1, B: Site 2, C: Site 3, D: Site 4) in the department of Cauca, Colombia, prior to the direct seeding implementation conducted between November and December 2022. For soil preparation and management in the study sites, we followed the protocol proposed by Piotrowski, Silva, and Piña-Rodrigues (2020). These images provide a baseline reference for the vegetation conditions before the restoration activities began.

TABLE 1 | Number of tree species and seed quantities sown at four restoration sites in the department of Cauca, Colombia, between November and December 2022. The number of tree species is categorised by seed size (large, medium and small), dispersal syndrome (anemochoric, autochoric and zoochoric) and ecological group (non-pioneers and pioneers).

	Site 1	Site 2	Site 3	Site 4	All sites
Number of tree species	38	30	32	28	45
Seed quantity (kg)	55.6	49.2	44.6	48.0	196.4
Seed size classes					
Large seeds	12	7	7	6	12
Medium seeds	7	7	6	6	10
Small seeds	19	16	19	16	23
Seed ecological group					
Pioneer species	17	15	17	15	19
Non-pioneer species	21	15	15	13	26
Seed dispersion group					
Anemochoric	3	7	7	7	7
Autochoric	4	2	2	2	4
Zoochoric	31	21	23	19	34

hydrated in regular tap water from the local water supply for 24h before being sown. For seeds in dormancy, breaking was done through mechanical scarification or soaking in water (Table S1). We trained the local community to distribute and manually sow seeds in the field. Manually sowing involves placing seeds directly into prepared planting holes or furrows, ensuring proper soil contact and spacing to promote germination. We provided practical training to local community members (i.e., men, women and children) organised through local associations. Most participants were smallholder farmers familiar with agriculture, contributing voluntarily to the project. The seeds were broadcast entirely by hand on the surface and then covered with soil. Larger seeds were manually placed individually in the soil at different depths. Sowing depth varied from 1 to 5 cm depending on seed size. Large seeds were sown at depths of 3 to 5 cm, medium seeds at 1 to 2 cm and small seeds were placed superficially, just beneath the soil surface.

The restoration sites had different sizes and received different quantities of seeds and species with ecological attributes (Figure S1). A total of 45 species and 196.1 kg were sown in all restoration sites, with 22 species shared among all sites (Table S1). At Site 1, we used the largest number of species (38) and seed quantity (55.6 kg). At Site 4, we sowed the lowest number of species (28), and for Site 3, the lowest seed quantity (44.6 kg). The variability in the types and quantities of species sown depended on the availability of seeds collected throughout the project and the phenology of the species, as seeding relied on whether the trees were fruiting at the time of collection. Seed sizes and dispersion syndrome varied among study sites (Table 1). We controlled leaf-cutter ants in all sites by the distribution of the biological bait Hormix SB. No irrigation was done after the seeding.

2.4 | Experimental Design and Monitoring

We monitored seed emergence and seedling survival in plots of 25 × 4 m (100 m^2). We established four plots in smaller sites (1 and 2) and five plots in the larger ones (3 and 4). The plots were arranged systematically, meaning they were spaced at regular intervals, with at least 20 m between them, to ensure that different slope variations and vegetation covers were represented, capturing the full heterogeneity of each site. Seedling emergence, defined as the number of seeds that successfully emerged in the field after being sown, was monitored at 90 and 150 days after sowing, using 1 × 1 m (1 m^2) quadrants randomly placed across the plots. We used four quadrants at 90 days and six quadrants at 150 days. Botanical identification of the seedlings was performed based on their leaf characteristics. We chose not to monitor during the first 30 days to minimise disturbance during the critical early stages of seed germination and establishment at the restoration sites. For the vegetation attributes in the final monitoring phase, we measured the height of seedlings (i.e., individuals with height < 50 cm), as these represent the early establishment phase. Weed cover and bare soil were visually estimated across the entire 1 m^2 sampling plot. In the 100 m^2 plot, we measured height and diameter at collar height for all saplings (> 50 cm in height), which represent more advanced growth stages beyond the seedling phase. We used this inventory to calculate the density of saplings and seedlings per hectare.

We recorded establishment and maintenance costs for direct seeding throughout the study period at each site. This included all material, machinery and labour costs associated with seed collection, site preparation, manual weeding and the applications of fertilisers, herbicides and formicides.

3 | Data Analysis

We calculated emergence and seedling survival at the species level across all sites. For the purpose of reporting overall species performance, we pooled the data from all sites. We calculated emergence percentage as the ratio between the number of seeds that emerged in the field and the total number of seeds sown per parcel (Piotrowski et al. 2023), with a mean emergence percentage and its associated standard error reported. We calculated seedling survival as the number of seedlings present at 150 days divided by the number of seeds that had emerged at 90 days (James, Svejcar, and Rinella 2011). All individuals were categorised as either sowed or regenerating naturally. Differentiating between these two categories was straightforward in the field, as the sown seeds were placed manually in holes or furrows, while naturally regenerating individuals emerged outside these rows. Additionally, the species composition of the sown seeds differed from those regenerating naturally, minimising confusion.

We used analyses of variance, ANOVA (Fisher 1992), with site as the sole predictor variable to compare emergence, survival, weed cover, bare soil and vegetation attributes (i.e., density of saplings, density of seedlings, saplings height, seedling height and diameter at collar height) among the four sites, also including the mean variable and its standard error. We used Tukey's Honest Significant Difference (HSD) test for multiple comparisons to determine which group means were significantly different, with a significance level of 0.05 (Tukey 1949). Variables expressed as a percentage were transformed by a square root function before analysis to meet assumptions of normality and homogeneity of variances (Gotelli and Ellison 2021). To explore the association between seed size, dispersal syndrome and ecological group with species emergence, we analysed the number of species per category using a Chi-squared test, with a significance level of 0.05 (Zar 2010). We excluded from the analyses all those species with null emergence and individuals from natural regeneration. All statistical analyses were performed using R software (R Core Team 2021).

4 | Results

We sampled in the four sites 1390 individuals belonging to 51 species, 44 genera and 32 families. At 150 days after direct seeding, 30 species emerged, 67% of the total seeded species. Mean emergence percentage for all species across sites was 1.7 ± 0.4 (standard error), with a range from 0% to 19% (Table 2). The highest mean emergence was observed at Site 1, where Guayaba (*Psidium guajava*) (19%), Roble (*Quercus humboldtii*) (11%) and Guamo Churimo (*Inga densiflora*) (6%) were the species with the highest percentage. The lowest mean emergence was evidenced at Site 2, where higher values were observed for Guayaba (6%), Roble (3%) and Achiote (*Bixa orellana*) (2%). At Site 3, the species that had the highest emergence were Roble (16%), Guamo Churimo (13%) and Tachuelo (Zanthoxylum sp.) (5%). At Site 4, Guamo Churimo, Matachande (*Bocconia frutescens*) and Roble had the highest emergence with 17%, 9% and 7%, respectively.

Survival rates ranged from 0% to 100%, with a mean of 24 ± 3 (Table 2). At Site 1, Chontaduro (*Bactris gasipaes*), Yolombo (*Panopsis polystachya*), Caimito (*Pouteria caimito*) and Lúcuma (*Pouteria* lucuma) had 100% survival. At Site 2, the species that obtained 100% of survival were Matachande and Arrayán Común (*Myrcia popayanensis*). At Site 3, Frutillo (*Solanum umbellatum*), Yolombo and Vainillo (*Senna spectabilis*) were the species with 100% survival. At Site 4, the highest survival rate, with 100%, was recorded for the species Guayaba.

Fifteen of the total 45 species did not emerge in the sites (Table 2). Species that did not emerge (87%) had small or medium seeds; only Aguacatillo (*Persea caerulea*) and Palma Zancona (*Syagrus sancona*) were the only large-seeded species that did not emerge with large seeds. Sites 2 and 4 had the highest percentage of species that did not emerge, 67% and 64%, respectively. In addition, six species were naturally dispersed and established across the sites, and Salvia Dulce (*Salvia venulose*) naturally established across all sites (Table S2).

For the vegetation attributes 150 days after sowing, the sapling density ranged from a mean of 496 ± 39 (at Site 3) to 5550 ± 366 individuals per hectare (at Site 1). Mean vegetation height was considerably higher at Site 4 (0.8 ± 0.4 m); for this site, the species Matachande showed height values from 0.28 to 2.1 m. However, the Matachande growth rate was not similar at other study sites (Figure S2). Other species with mean sapling height greater than 1 m were Balso Blanco (*Heliocarpus americanus*) at sites 1 and 4. In contrast, Achiote and Guayaba showed a high emergence, but sapling height was low, varying from 0.08 to 0.23 m (Table S3). Diameter at collar height with an average of 4.5 ± 0.5 cm was significantly different at Site 1, where non-weed cover was reported.

TABLE 2 | Number of species that have not emerged, mean and coefficient of variation (CV) for the percentage of seed emergence and survival after 150 days of sowing across four restoration sites. The table displays the mean values for each individual site, as well as an aggregated mean for all sites. The direct seeding was conducted in the department of Cauca, Colombia, between November and December 2022.

	Site 1	Site 2	Site 3	Site 4	All sites
Number of not emerged species	8	20	10	18	15
Emergence (%)	2.4	0.7	1.9	1.7	1.7
CV	(1.6)	(2.5)	(1.8)	(2.3)	(2.0)
Survival (%)	37	16	12	17	24
CV	(1.0)	(2.1)	(1.6)	(1.7)	(1.5)

At Site 3, weed cover had values greater than 79%. Moreover, the density of seedlings and the vegetation height were markedly lower at Site 2, where a higher percentage of bare soil was registered (Table 3). Zarza (*Mimosa pigra*) and Ricino (*Ricinus communis*) were the invasive species registered at sites 2 and 4, respectively.

We found that species with large seeds had higher emergence percentages compared with medium and small seeds (Figure 3A). The mean emergence percentage in large seeds was 6 ± 1, with a range from 0% to 17%. Species such as Guamo Churimo, Roble and Cedro Negro (*Juglans neotropica*) had higher emergence percentages among the large seed species. For the dispersal syndrome, zoochoric species evidenced higher emergence variation, with a mean emergence percentage of 6 ± 1, ranging from 0% to 19%, while anemochoric species had a mean of 5 ± 2 and varied from 0% to 6%. Finally, autochoric species had a mean emergence percentage of 3 ± 1, ranging from 0% to 3% (Figure 3B).

At Site 1, the emergence percentage was higher for anemochoric species than other dispersion syndromes; species Balso Blanco and Guayacán de Manizales (*Lafoensia acuminata*) were anemochoric species with the highest emergence percentage. For the ecological group, non-pioneer species were significantly different at Sites 1 and 2. In Site 3, the emergence percentage was moderate, and Site 4 shows higher variability but lower median values. In general, pioneer species performed better at Site 4 (Figure 3C).

The establishment and maintenance costs for the 150 days of the study period ranged from US$ 2145 (at Site 1) to US$ 2027 (at Site 2) per hectare (Table 4). Establishment costs constituted 84%–89% of the total costs. The most expensive input during the establishment was the tree seed cost (US$ 480–435 ha^{-1}) and topsoil fertilisers (US$ 437 ha^{-1}). For the maintenance, manual weeding represented 49%–61% of the subtotal costs (Table 4).

5 | Discussion

Many authors report a high seedling density in their direct seeding experiments; for instance, after 1–3 years, a seedling density of more than 15,000 ind. ha^{-1} has been sampled (Campos-Filho et al. 2013; Piotrowski et al. 2023). In contrast, unsatisfactory results after 2 years have been reported by Souza and Engel (2018); they obtained a density of 1265 ind. ha^{-1}. In our study, after

TABLE 3 | Mean vegetation attributes (±SE) after 150 days of sowing across four restoration sites. The direct seeding was conducted in the department of Cauca, Colombia, between November and December 2022.

	Site 1	Site 2	Site 3	Site 4
Density of saplings (ind. ha^{-1})	5550 ± 366^{a}	3750 ± 551^{b}	496 ± 39^{c}	708 ± 121^{c}
Saplings height (m)	0.3 ± 0.6^{a}	0.2 ± 0.3^{a}	0.3 ± 0.1^{a}	0.8 ± 0.4^{b}
Density of seedlings (ind. ha^{-1})	350 ± 27^{a}	25 ± 1^{b}	172 ± 47^{ac}	96 ± 34^{c}
Seedlings height (m)	0.8 ± 0.1^{a}	0.5 ± 0.1^{b}	0.6 ± 0.1^{b}	1.1 ± 0.2^{a}
Diameter at collar height (cm)	4.5 ± 0.5^{a}	1.0 ± 0.1^{b}	1.8 ± 0.3^{b}	0.6 ± 0.1^{b}
Weed cover (%)	0^{a}	14.5 ± 3.4^{b}	79.1 ± 2.5^{c}	5.9 ± 2.2^{d}
Bare soil (%)	10.7 ± 2.4^{a}	18.3 ± 4.5^{b}	6.0 ± 2.9^{a}	6.0 ± 3.2^{a}

Note: For each variable, different superscript letters denote statistically significant differences between land use types, according to Tukey's test ($p < 0.05$).

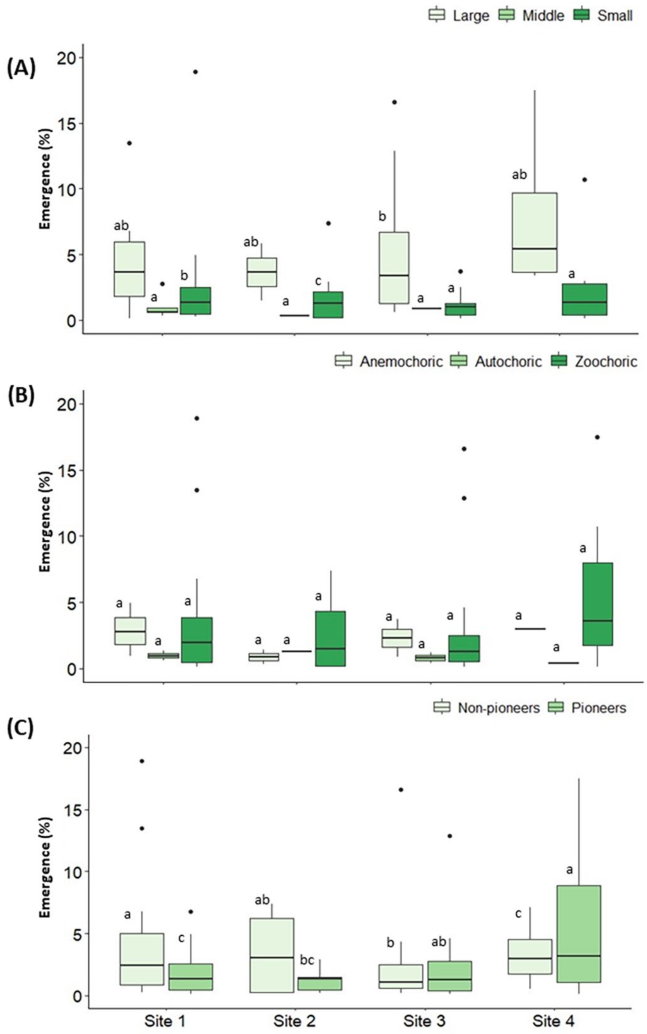

FIGURE 3 | Boxplots for emergence percentage at 150 days after sowing in relation to seed size (large, medium and small) (A), dispersion syndrome (anemochoric, autochoric and zoochoric) (B) and ecological group (non-pioneers and pioneers) (C), as part of the monitoring process. Seed emergence was monitored in 25 × 4 m plots (100 m^2). Four plots were established in the smaller sites (1 and 2) and five plots in the larger ones (3 and 4). Letters indicate significant differences in species emergence between restoration sites, determined through pairwise chi-squared tests.

TABLE 4 | Establishment and maintenance costs for direct seeding for the 150 days of the study[a]. The direct seeding was conducted in the department of Cauca, Colombia, starting activities in November 2022.

	US$ ha^{-1}			
	Site 1	**Site 2**	**Site 3**	**Site 4**
Establishment costs				
Manual land clearing	411	224	261	267
Mechanical soil preparation	321	320	489	409
Herbicide[b]	36	36	36	36
Herbicide application	50	50	50	50
Topsoil fertilisers	437	437	437	437
Fertilisers application	45	45	45	45
Trees seeds	480	470	435	450
Green manure seeds	119	119	119	119
Subtotal	1899	1701	1872	1813
Maintenance costs (150 days)				
Manual weeding	120	200	120	180
Herbicide	20	20	20	20
Herbicide application	50	50	50	50
Formicide	18	18	18	18
Formicide application	40	40	40	40
Subtotal	246	326	246	306
Total costs	2145	2027	2118	2119

[a]During the period of study, 1 US$ = 4500 COP. Labor costs averaged 13.3 US$ per 8 h working day.
[b]Herbicide = 36 US$ per 2 L (2 L ha^{-1}).

150 days of seeding, the density of saplings (5550 ind. ha^{-1}) and seedlings (350 ind. ha^{-1}) can be considered as acceptable only for Site 1. This assessment is based on two main criteria: (i) the values for both saplings and seedlings are considerably higher than those obtained in other sites within this study, where sapling densities range from 496 to 3750 ind. ha^{-1}, and (ii) these values, although lower than the densities reported in other studies with longer time frames, suggest successful early establishment given the short period of 150 days, indicating favourable conditions at Site 1 for seed emergence and sapling development. This result can be mainly related to the different initial soil conditions and land-use history; besides that, in Site 1, we used higher seeding density. According to recent investigations on direct seeding, a higher trees density can be expected in soils of better quality (Ceccon, González, and Martorell 2016; Freitas et al. 2019). We highlight that our results are restricted to the intervention time of 150 days and to the environmental conditions of our sites; thus, further assessments should be made to have a possible scaling-up of our results.

In Sites 2, 3 and 4, weeds emerged quickly after sowings, and the chemical treatments were inefficient in managing the invasive grass. The intense rain may have caused herbicide runoff, reducing its ability to function effectively. Previous studies have indicated that careful weeding before sowing and during the first year of establishment is essential to increase the chance of direct seeding success (Willoughby and Jinks 2009; Souza and Engel 2018). In these same sites, the green manure was not successfully established due to the insects' attack or weed competition.

Our results indicate that the outcomes of direct seeding can be variable, affecting the achievability of restoration targets. For instance, our Site 4 had different plant covers 6 months after sowing (Figure 4). Thus, for all sites, we did a complementary seedling plantation to occupy patches with reduced seedling densities, following recommendations from previous research (Meli et al. 2018). One strategy to improve the direct seeding performance could be choosing species with higher emergence and survival rates; also, difficult-to-seed species can be supplemented by seedling planting (Souza and Engel 2018; Freitas et al. 2019). Of the 45 species that were used in our study, those that performed best per seeding site are presented in Table S3.

In this study, we found that species with large seeds were more appropriate for the direct seeding technique. Similar results have been reported by other research groups (Camargo, Ferraz, and Imakawa 2002; Ceccon, González, and Martorell 2016; Souza and Engel 2018; Piotrowski et al. 2023). Overall, large seeds can tolerate extreme conditions; they contain more reserves and have higher quantities of secondary compounds that can inhibit predation (Camargo, Ferraz, and Imakawa 2002). Another factor that could have affected the emergence of small seeds was the intense rains that followed direct seeding. These rains may have washed away the seeds on the steep slopes of our mountain sites. In addition, our study did not test seed viability, and therefore some seeds may fail to emerge due to low seed quality. In future projects, to avoid the low-quality seeds, recent standards for native seeds in ecological restoration should be used (Cross, Pedrini, and Dixon 2020; Pedrini and Dixon 2020).

For the dispersal syndromes, we observed that pioneer species that are associated with small seeds had lower emergence among direct seeded sites. Smaller seeds have fewer resources overall, which limits their capacity to sustain germination and seedling establishment (Dalling and Hubbell 2002; Del Castillo and Ríos 2008). This low emergence could also be due to the seeds of pioneer species requiring special environmental conditions for germination (i.e., soil moisture or temperature) that were not achieved during our investigation (Souza and Engel 2018). Particularly, the dispersion syndromes did not significantly affect the emergence of the species.

The cost of forest restoration in Colombia is unclear; the values reported in the literature for tree plantation and maintenance during the first year vary between US$ 740 and 18,400 ha^{-1} (Murcia and Guariguata 2014). Besides, there is no information on the cost of direct seeding to restore ecosystems in Colombia. In the tropics, most direct seeding project costs are from Brazil and do not apply to Colombia. For example, the costs ranged from US$ 742 to 912 ha^{-1} for the seeding and maintenance of five species in the first 2 years in São Paulo (Engel and Parrotta 2001). In the Xingu region, located in Brazil, it was reported a cost per hectare of US$ 1845 taking care of the hectare for 3 years (Campos-Filho et al. 2013). Another study, showing 31 species, obtained a cost of US$ 1822 ha^{-1} for establishing and maintaining a restoration site for 2 years (Souza and Engel 2018). Our establishment and maintenance costs were higher than those studies using direct seeding in Brazil, primarily due to the mountainous topography of our sites, which increased the time required for soil preparation, weeding and herbicide and fertiliser applications.

Our results suggest that direct seeding for the restoration of degraded tropical mountain ecosystems requires a different approach than lowland temperate regions. Regarding ecological results of seeding in mountainous areas, it is difficult to control outputs as there are many variable factors, including slope inclination, soil type, climate, altitude, land-use history and vegetation cover. Direct seeding can be complemented with other tree-planting practices used in forest restoration projects (Camargo, Ferraz, and Imakawa 2002; Cole et al. 2011).

To better capitalise on the benefits of direct seeding, it is recommended to combine the direct seeding with agroforestry and other restoration approaches applied in mountain landscapes, such as terrace farming, hedgerow intercropping and

FIGURE 4 | Direct seeding outputs after 150 days in Site 4, located in the department of Cauca, Colombia, where direct seeding was conducted in December 2022. (A) Area invaded by Ricino (*Ricinus communis*), (B) Area after manual weeding with native seedlings measuring more than one meter in height, (C) Area covered by invasive grass and saplings with heights less than 50 cm, (D) Area affected by soil erosion and where the green manure was attacked by an insect.

sloping agricultural and technology (Tacio 1993). Recently, the combination of remote sensing and highly precisely guided unmanned vehicles such as drones has offered the possibility of expanding the use of direct seeding to large areas and hard-to-reach places in the mountains (Castro et al. 2021). However, this approach also presents several challenges, such as ensuring accurate seed placement, maintaining seed viability during aerial deployment and dealing with environmental factors like wind and terrain irregularities that can reduce effectiveness. Additionally, the cost of drone technology and limited battery life pose logistical constraints for large-scale applications (Castro et al. 2022). Despite these challenges, the potential of drones remains promising, especially as technology and techniques continue to improve.

6 | Implications for Restoring Mountain Ecosystems

Our results suggest that direct seeding may be a useful technique to restore tropical mountains. However, we observed that these ecosystems can be sensitive, and several limitations must be addressed before recommending upscaling as a restoration intervention. We discuss some of these limitations and recommendations to inform and improve future restoration research and practice.

First, species selection is key. It is critical to identify high-quality seeds and to understand the species responses under the different mountain soil conditions. We evaluated 45 tree species, but only 30 species (67%) emerged after 150 days of sowing, and the emergence percentage was quite variable across sites. In this line, and secondly, minimising soil disturbance to prevent erosion during site preparation is critical. Third, this technique requires careful timing with the rainy season to avoid herbicide runoff and weed growth. In tropical mountains, direct seeding requires extensive weed control during the first months to ensure better native seedling survival and growth rates.

Based on the results of this study, the following management practices are recommended to improve the effectiveness of direct seeding in degraded montane areas: (1) Synchronise seeding with climatic conditions, ensuring that it coincides with the rainy season to provide sufficient moisture for germination; (2) avoid the use of heavy machinery or tractors during soil preparation to prevent soil erosion and compaction; (3) use high-quality seeds with known germination rates to increase the probability of successful establishment; (4) select species carefully, focusing on those with strong field performance in terms of growth and canopy development to ensure effective site recovery; and (5) protect seeds from predation and environmental stress by applying techniques such as hydromulching or seed coatings, which reduce desiccation, deter seed loss and provide essential nutrients to facilitate germination (Palma and Laurance 2015; Pedrini et al. 2020). We expect these recommendations will be useful for restoration researchers and practitioners interested in restoring tropical mountain ecosystems.

Finally, we call attention to the need for long-term monitoring at mountain restoration sites. Long-term monitoring is crucial to better understand direct seeding results when using different species in degraded sites and thus provide help for public policies focused on restoration, particularly in countries with high extents of mountain ecosystems, such as Colombia.

Acknowledgements

We acknowledge PUR Projet for supporting the project. We also acknowledge the staff from Corporación Social Ambiental y Agroforestal para la Vida (CORSAVIDA) and the farmers from the rural communities of Popayán and Cajibío, Cauca, who allowed the restoration implementation and contributed to seed provision. We recognise and honour the Indigenous communities of this region as the traditional custodians of these lands. Finally, we thank Ritikaa Gupta for her help in editing and translating this paper, and Pablo Figueiredo (Gavilán Mayor) for his support in the statistical analysis of the data.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.