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RESEARCH ARTICLE

Linking topography, soil variability, and early successional vegetation in abandoned gold mines in the tropical rainforest of Colombia's Chocó Biogeographic region

Hamleth Valois-Cuesta[1], Carolina Martínez-Ruiz[2,3], Zulay Q. Valoyes[1]

Soil fertility heterogeneity is one of the main factors affecting early recovery and plant succession toward a target plant community. This study examined the influence of topography on the diversity and composition of plant communities established in areas degraded by opencast mining in Chocó, Colombia. Soil fertility and plant community were characterized in the four topographic formations identified in the abandoned mines: plains (PL), slopes (SLP), floodplains (FP), and sand and gravel mounds (SGM). Topographic formations did not result in significant differences in soil properties. However, a gradient of fertility and vegetation cover was observed: from the SGM, with less fertile soils and little vegetation, to the PL, SLP, and FP, with the most fertile soils and greater vegetation cover and density. The species composition found in PL, SLP, and FP was similar but differed from that of SGM. These results suggest that the SGM does not promote early revegetation in the mines. However, experimental studies are necessary to determine how topographic formations and soil conditions resulting from mining should be managed to facilitate the early recovery of vegetation and the ecological restoration of areas affected by mining.

Key words: ecological restoration, gold mining, natural revegetation, soil nutrients, topography, tropical rainforests

Implications for Practice

- Knowledge of the variability and quality of soil properties in areas disturbed by mining may improve management practices for the establishment of plants in abandoned mines that are subject to ecological restoration.
- From a mining land management perspective, it is important to promote interventions resulting in large plain and floodplain areas, as these topographic formations facilitate the conservation of nutrients in the soil and passive and active revegetation in the mining landscape.
- Sand and gravel mounds should be removed from the abandoned mines to promote the passive or active restoration of these critical areas, as these topographic formations do not promote early natural revegetation.

Introduction

The biogeographic Chocó in Colombia, having the highest rainfall level in the world, is one of the most biodiverse regions of the planet (Rangel-Churio 2004; Pérez-Escobar et al. 2019). The outbreak of illegal gold mining due to global demand, however, is a threat to the conservation of natural tropical rainforests (Alvarez-Berríos & Aide 2015; Siqueira-Gay & Sánchez 2021). In this region, mining activity has increased significantly over recent years due to the use of heavy machinery, contributing to the loss of forest cover (Valois-Cuesta & Martínez-Ruiz 2016). This scenario has promoted interest in the ecological restoration of these strategic ecosystems for wildlife conservation (Murcia & Guariguata 2014; Valois-Cuesta & Martínez-Ruiz 2016).

Theoretically, disturbed ecosystems can gradually recover over time (Bradshaw 1984), but, since mine wastes are invariably poor in plant nutrients and may be toxic to plants, and have physical shortcomings that are hardly suitable for plant growth, natural colonization may be extremely slow (Ellery & Walker 1986; Martínez-Ruiz et al. 2001). Therefore, understanding how natural succession operates at distinct spatial and temporal scales may help in the identification of ecological mechanisms and processes to facilitate the early recovery of these ecosystems

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[1]Facultad de Ciencias Naturales, Programa de Biología, Universidad Tecnológica del Chocó, Cra. 22 N° 18B-10, Nicolás Medrano, Quibdó, Colombia
[2]Area de Ecología, Dpto. Ciencias Agroforestales, iuFOR (Instituto Universitario en Gestión Forestal Sostenible), E.T.S. de Ingenierías Agrarias, Universidad de Valladolid, Campus La Yutera, Avenida Madrid 50, 34071, Palencia, Spain
[3]Address correspondence to C. Martínez-Ruiz, email carolina.martinez.ruiz@uva.es

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(Bradshaw 1997; Walker & del Moral 2003; Valois-Cuesta et al. 2022).

Although different restoration strategies have been developed in some tropical countries, a knowledge gap continues to exist regarding successful results for post-mining restoration projects (Román-Dañobeytia et al. 2021; Martins et al. 2022). Therefore, knowledge of natural revegetation processes is vital to developing tools to facilitate the ecological restoration of disturbed ecosystems, especially in areas where primary succession is the starting point (Hobbs & Norton 1996; Pastorok et al. 1997; Walker & del Moral 2003). Areas disturbed by mining experience dramatic changes in soil conditions, which may determine the successive colonization of plant functional groups since the availability of soil nutrients for plants varies during the natural succession process (Walker & del Moral 2003; Walker et al. 2010; Ramírez-Moreno et al. 2019).

The spatial distribution of soil fertility is a limiting factor for early revegetation of disturbed areas in which soil has been dramatically impacted, as occurs in open-pit mines (Tilman 1985; Moreno-de las Heras et al. 2008, Román-Dañobeytia 2021). Topography is one of the main factors promoting the spatial heterogeneity of soil nutrients. For example, lands with steep slopes (SLP) often experience more erosion, have and retain fewer nutrients, and provide fewer microsites for seed retention, as compared to flat lands (Hoogendoorn et al. 2016), and areas with concave shapes, which tend to accumulate more nutrients than these convex areas (Walker & del Moral 2003).

In open-pit gold mining, backhoes are often used to modify the original topography of the land, resulting in artificial topographic formations (plains [PL], SLP, floodplains [FP], and sand and gravel mounds [SGM]; Fig. 1). These new topographic formations may cause changes in the soil fertility distribution and may thereby affect the early revegetation (Valois-Cuesta & Martínez-Ruiz 2017). Therefore, some authors have proposed that the study of mechanisms that influence the distribution of soil fertility is important to understanding how natural revegetation occurs in disturbed areas by mining (Martínez-Ruiz & Marrs 2007; Ramírez-Moreno et al. 2019; López-Marcos et al. 2020).

If topography determines variations in soil fertility and vegetation (Kumhálová et al. 2011; López-Marcos et al. 2020), then, how does early revegetation occur in different topographic formations resulting from mining activity in the tropical rainforests of Chocó in Colombia? And if differences do exist, are these differences in vegetation related to variations in soil fertility between topographic formations in the mines? The initial hypothesis is that topographic formations that conserve or promote greater soil fertility also present greater plant diversity and cover in early plant communities.

The objective of the study was to determine the relationship between topography, soil physical and chemical properties, and vegetation at the early stage of the natural regeneration of gold mines in the tropical rainforest of Chocó in Colombia.

Methods

Study Site

The study took place from June to December 2014 in Raspadura (lat. 5°13′17″N, long. 76°38′37″W), Unión Panamericana, Chocó, Colombia. Raspadura is situated in the Chocó Biogeographic region of western Colombia (Fig. 1). This region is characterized by having annual rainfall exceeding 11,000 mm, an average annual temperature of 26°C, and a relative humidity of 80% (Poveda et al. 2004). The vegetation in Raspadura is typical of a tropical rainforest (Poveda et al. 2004). The natural forest matrix (reference ecosystem) shows a floristic diversity of 4.5 (Shannon), with the dominance of tree, shrub, and epiphytic species such as *Ossaea bracteata*, *O. spicata*, *Tococa guianensis* (Melastomataceae), *Palicourea seemannii*, *Psychotria longicuspis*, *P. poeppigiana* (Rubiaceae), *Anthurium lancea*, *Dieffenbachia plowmanii* (Arecaceae), *Dicranopygium cuatrecasanum* (Cyclanthaceae) and *Qualea lineata* (Vochysiaceae). The mining areas, after 24 years of natural succession, are less diverse (Shannon 2.1–2.9) and dominated by herb and shrub species such as *Andropogon bicornis* (Poaceae), *Lycopodiella cernua* (Lycopodiaceae), *Sticherus bifidus* (Gleicheniaceae), *Cyperus luzulae*, *Eleocharis interstincta*, *Rhynchospora tenerrima* (Cyperaceae), *Clidemia sericea* (Melastomataceae), *Hypolepis repens* (Dennstaedtiaceae), *Sauvagesia erecta* (Ochnaceae), and *Xyris jupicai* (Xyridaceae) (Rangel-Churio & Rivera-Díaz 2004; Valois-Cuesta & Martínez-Ruiz 2017; Valois-Cuesta et al. 2022). The richness of plant species in the Chocó territory has been a source of goods and services for the subsistence of the peoples settled in the region (Valois-Cuesta & Martínez-Ruiz 2017).

Fieldwork was carried out in two mines, 5 years after the mining activity had concluded (Fig. 1). Open-pit mining was carried out at both sites, using backhoes to extract large volumes of underground material, which was washed on metal filters with the help of high-pressure pumps (Fig. 2A). The two mines under study are representative of the type of gold mining taking place in the Chocó region (Fig. 2) and they are characterized by having various topographic formations (PL, SLP, FP, and SGM; Fig. 2B–D). The representativeness of the topographic formations (in square meter per hectare and percentage) in 10 ha of the mining landscape was: SGM (6905.1 ± 214.3 m^2/ha; 69%), FP (1828.5 ± 129.8 m^2/ha; 18.3%), PL (645.5 ± 122.3 m^2/ha; 6.5%), and SLP (620.9 ± 84.3 m^2/ha; 6.2%), with SGM and FP being significantly more abundant (Kruskal–Wallis = 32.7; $p < 0.0001$). The soils of these mines are poor in nutrients, acidic, and have a high concentration of aluminum (Valois-Cuesta & Martínez-Ruiz 2017; Ramírez-Moreno et al. 2019).

Vegetation and Soil Sampling

Ten 20 × 20 cm plots were inventoried in each topographic formation (five per mine and topographic position; $n = 40$ plots). In each plot, the number of individuals per vascular plant species (density), total plant cover (%), and bare soil surface (%) were recorded. The taxonomic identity of each species was determined using specialized literature (Gentry 1996), comparison with herbarium specimens, and through the collaboration of

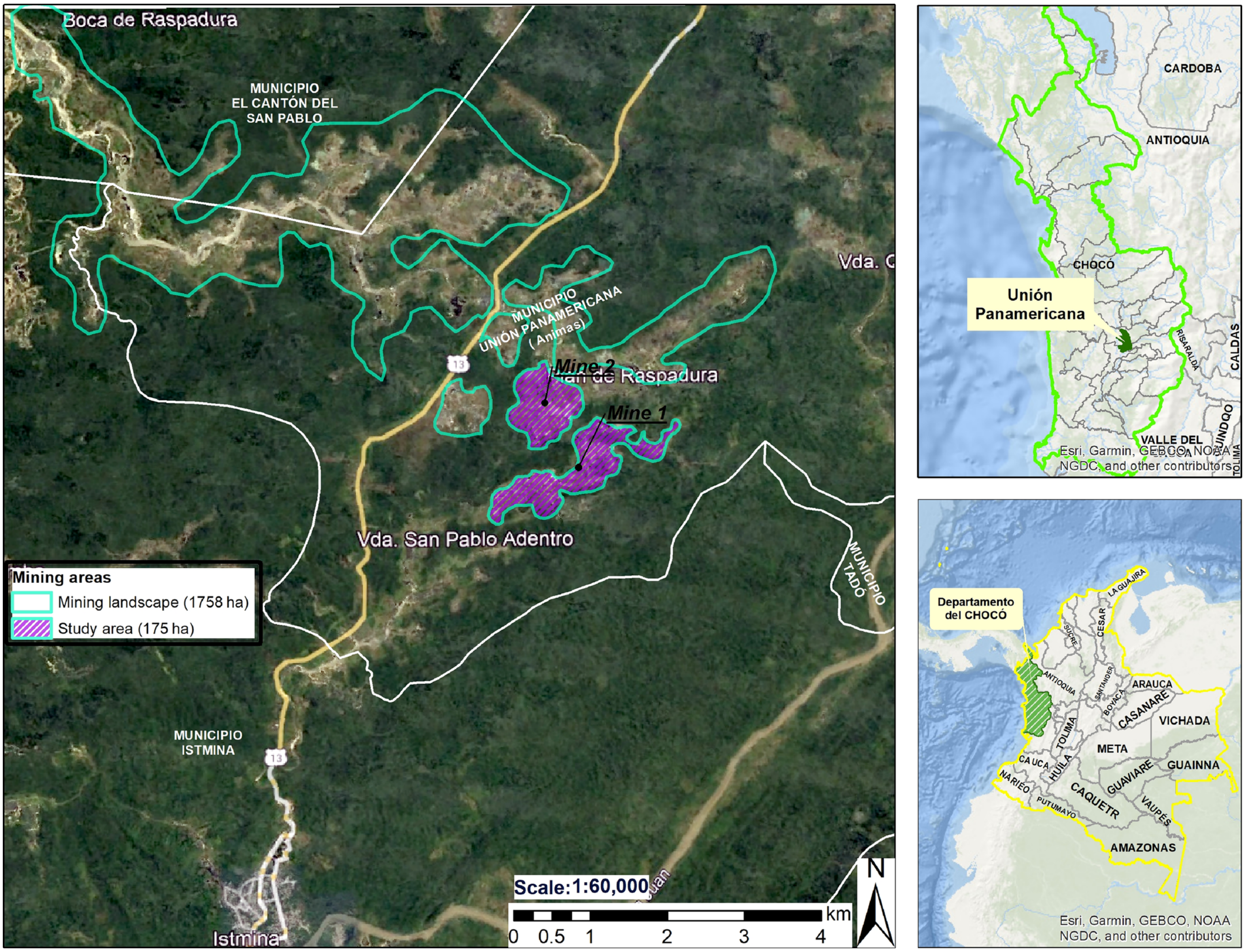

Figure 1. Location of the mines under study within the mining landscape of the municipality of Unión Panamericana, Chocó, Colombia.

Chocoan flora specialists. Scientific names of the species were confirmed in the Plant List (http://www.theplantlist.org). All specimens were deposited in the CHOCÓ Herbarium and their classification was based on the works of the Angiosperm Phylogenetic Group (Chase & Reveal 2009; Haston et al. 2009).

Two composite soil samples were analyzed in the laboratory per topographic formation (one per mine and topographic position; $n = 8$ samples). Each composite soil sample was the result of combining five subsamples (five per mine and topographic position; $n = 40$ subsamples), which were obtained from each plot where the vegetation was inventoried. These subsamples were taken with a soil auger of 8 cm in diameter and 20 cm deep.

The composite soil samples were analyzed using the following methods: texture (Bouyoucos method); effective cation-exchange capacity (CEC; saturation with ammonium acetate quantification method: volume); pH (extraction method: soil/water [1:1]; quantification method: potentiometric); Al^{3+}, Mg^{2+}, Ca^{2+}, K^{+} (extraction method with 1 N ammonium acetate at pH 7; quantification method: atomic absorption), available phosphorous (P; extraction method: B–Bray II, quantification method: using ascorbic acid as a reducing agent), organic matter (OM; extraction method: B-Walkley Black-wet oxidation; quantification method: volumetric), and total nitrogen (N; Kjeldahl method).

Data Analysis

Species richness (S), density, total plant cover, and bare soil percentages, and Margalef (D_{Mg}), Shannon (H'), and Simpson ($1/D$) diversities were calculated for each vegetation inventory ($n = 40$, 10 per topographic formation). Shannon (H') and Simpson ($1/D$) diversity indices were also calculated for the entire plant community in each topographic formation, and species richness was calculated with the Chao1 estimator (Colwell 2013).

Differences in floristic composition between topographic formations were calculated with the Jaccard (Equation 1) and Sørensen (Equation 2) indices and their probabilistic estimates ($\widehat{J}_{abd}$ and $\widehat{L}_{abd}$, respectively) proposed by Chao et al. (2005):

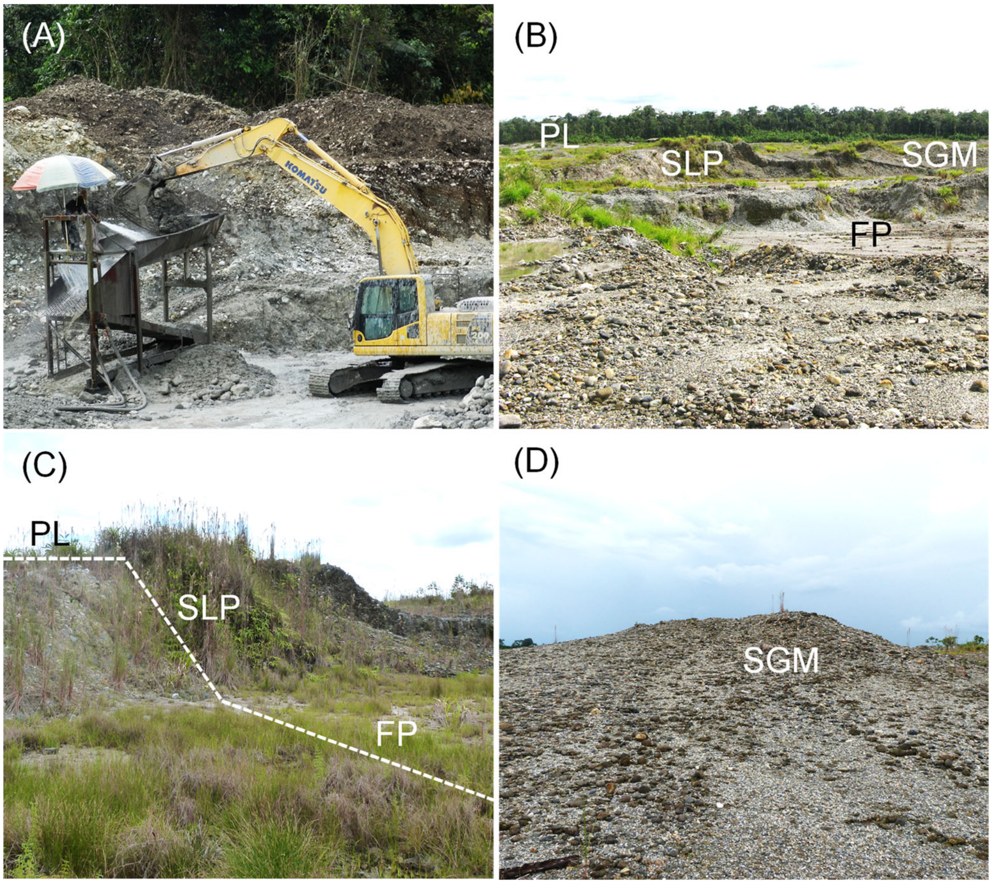

Figure 2. Gold extraction with heavy machinery (A) and distribution of the four topographic formations (PL = plain, SLP = slope, FP = floodplain, SGM = sand and gravel mounds) (B–D) in the gold mines of Raspadura, Chocó, Colombia.

$$J_{\mathrm{abd}} = \frac{\mathrm{UV}}{(U+V-\mathrm{UV})} \tag{1}$$

$$L_{\mathrm{abd}} = \frac{2\mathrm{UV}}{(U+V)} \tag{2}$$

where U and V represent the total abundance of each plant community (1 and 2, respectively), and UV represents the abundance of shared species. Both indices reach 1 for identical floristic composition and tend to 0 for disjoint composition.

The representativeness of each species in each topographic formation was calculated using the Ecological Importance Index (EII; Ramírez 2006). This index is obtained by the sum of the relative density (density of the species divided by the sum of the densities of all species) and the relative frequency of each species (absolute frequency of the species divided by the sum of the frequencies of all species); that is, EII = relative density + relative frequency. The absolute density for a species in each topographic formation was calculated as the sum of all of the individuals of that species found in the ten 20×20 cm plots evaluated for each specific topographic formation. The absolute frequency was calculated as the sum of the number of plots where that species was found divided by the 10 evaluated plots (Ramírez 2006; Villareal et al. 2006).

Statistical differences between plant communities (topographic formations) in terms of the number of species, genera, and families were assessed using the Chi-square test. The influence of topographic formations (fixed effect) on the soil properties, Margalef (DMg), Shannon (H') and Simpson ($1/D$) diversities, richness (S), density, plant cover, and bare soil were analyzed using linear mixed models (LMM; Pinheiro & Bates 2000) with the restricted maximum likelihood method (Richards 2005); in all cases, the plot was included as the random effect. The ANOVA of each selected LMM was used to assess the significance of the model. Finally, working over the model matrix, multiple pairwise comparisons were carried out, using the Bonferroni correction to adjust for the significance level of each t test (Sokal & Rohlf 1995).

A principal component analysis (PCA) was performed to identify the underlying gradient in the soil properties according to the topographic formations. A second PCA was performed to relate vegetation variables (density, richness, diversity, and cover) to the soil properties of the topographic formations. Both PCAs were applied to the matrix of the global data, that is, one per topographic formation.

Analyses of plant species richness and diversity were made in Estimates 9.1 (Colwell 2013), whereas statistical analyses were implemented in the R software environment (version 4.1.2; R Core Team 2021), using the nlme package for LMM (3.1-152; Pinheiro et al. 2021), and the vegan package for multivariate analyses (2.5-7; Oksanen et al. 2020).

Results

Soil Properties in the Topographic Formations

The physical and chemical properties of the soil did not vary significantly between topographic formations (Table 1), except for Mg^{2+}, which was the highest in the FP. Nevertheless, the PCA revealed the underlying gradient in soil properties, from the SGM that had sandier soils and lower nutrient content than the PL and SLP topographic formations, where the soil was more fertile; FP had an intermediate position with soils having the highest Mg^{2+} content (Fig. 3).

Vegetation in the Topographic Formations

A total of 11 early successional vascular plant species were recorded during the vegetation survey. The richness estimator, Chao 1, indicated that the sampling effort was appropriate to record most of the species found in the topographic formations (Table 2). All recorded species were ruderal plants belonging to the Cyperaceae (*Elecharis filiculmis*, *E. interstincta*, *Rynchospora tenerrima*, *R. pubera*, *R. exaltata*, and *Scleria secans*), Gentianaceae (*Chelonanthus alatus*), Gleicheniaceae (*Sticherus bifidus*), Lycopodiaceae (*Lycopodiella cernua*), Melastomataceae (*Miconia reducens*), and Poaceae (*Andropogon bicornis*) families. Among them are some woody species (*M. reducens*), some with sub-woody stems (*L. cernua*), and some ferns (*S. bifidus*). The others are mostly perennial herbs, except for *C. alatus* (annual herb) or *R. tenerrima* (annual or perennial herb).

Statistical differences were found among topographic formations in the number of individuals, richness (S), Margalef (D_{Mg}), Simpson ($1/D$) diversities, total plant cover, and bare soil (Table 2). The SGM had the lowest number of individuals, S, D_{Mg}, $1/D$, total plant cover, and the highest bare soil of all of the topographic formations. The number of families, genera, and species (observed and estimated, Chao 1), as well as global diversity (Shannon and Simpson), were also lower in the SGM than in the other topographic formations; however, this difference was not statistically significant.

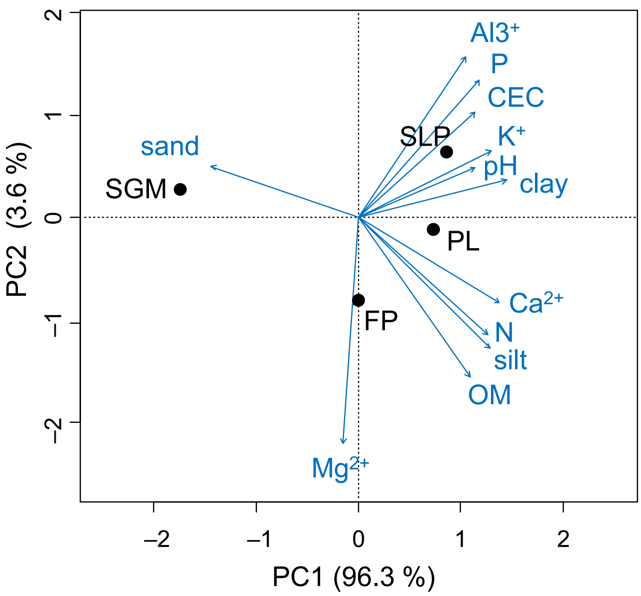

Figure 3. Principal components analysis (PCA) of soil properties in the different topographic formations (FP, floodplain; SGM, sand and gravel mounds; PL, plain; SLP, slope) in the gold mines of Raspadura, Chocó, Colombia. Abbreviations as in Table 1.

All topographic formations had more bare soil than soil covered with vegetation (Table 2), but the difference was only significant ($p < 0.05$) in SLP and SGM.

Regardless of the topographic formation type, the most representative species (EII) were: *A. bicornis* (208.5, 26.1%), *L. cernua* (208.2, 26.0%), and *S. bifidus* (125.8, 15.7%); followed by *R. tenerrima* (53.7, 6.7%), *E. filiculmis* (48.6, 6.1%),

Table 1. Physical and chemical properties of the soil in the different topographic formations (PL = plain, SLP = slope, FP = floodplain, SGM = sand and gravel mounds), in gold mines of Raspadura, Chocó, Colombia. F-value and significance (*$p < 0.05$) of the ANOVA applied to each linear mixed model. Different letters indicate significant differences between pairs of topographic formations with the Bonferroni test. Cation-exchange capacity (CEC).

		Topographic formations				*ANOVA*
Soil properties	*Unit*	*PL* (n = 2)	*SLP* (n = 2)	*FP* (n = 2)	*SGM* (n = 2)	(F, p)
Sand	%	54.0 ± 2.00	54.0 ± 4.00	58.0 ± 26.0	81.0 ± 1.00	1.19
Silt	%	27.0 ± 1.00	25.0 ± 1.00	28.0 ± 18.0	13.0 ± 1.00	0.59
Clay	%	19.0 ± 3.00	21.0 ± 5.00	14.0 ± 8.00	6.00 ± 0.00	3.94
pH	dS/m	4.40 ± 0.50	4.20 ± 0.00	4.00 ± 0.50	3.90 ± 0.05	0.34
Organic matter (OM)	%	1.50 ± 0.93	0.75 ± 0.17	1.17 ± 0.74	0.24 ± 0.03	0.81
Aluminum (Al^{3+})	cmolc/kg	1.40 ± 0.70	2.00 ± 0.50	1.30 ± 0.10	1.15 ± 0.03	0.87
Calcium (Ca^{2+})	cmolc/kg	0.05 ± 0.02	0.05 ± 0.01	0.05 ± 0.02	0.03 ± 0.00	0.43
Magnesium (Mg^{2+})	cmolc/kg	0.04 ± 0.01a	0.06 ± 0.02a	0.22 ± 0.04b	0.07 ± 0.01a	18.56*
Potassium (K^+)	cmolc/kg	0.05 ± 0.01	0.07 ± 0.01	0.05 ± 0.02	0.03 ± 0.00	3.00
CEC	meq/100 g	1.55 ± 0.65	2.15 ± 0.45	1.60 ± 0.10	1.25 ± 0.05	1.02
Phosphorus (P)	mg/kg	4.48 ± 2.50	4.50 ± 1.50	2.50 ± 0.50	2.50 ± 0.50	0.59
Total nitrogen (N)	%	0.11 ± 0.04	0.06 ± 0.06	0.06 ± 0.06	0.01 ± 0.01	4.35

Table 2. Vegetation variables in the topographic formations (PL = plain, SLP = slope, FP = floodplain, SGM = sand and gravel mounds) of gold mines of Raspadura, Chocó, Colombia. *F*-value and significance (*$p < 0.05$; ***$p < 0.001$) of the ANOVA applied to each linear mixed model, and χ^2 test (for the number of families, genera and species). Different letters indicate significant differences between pairs of topographic formations with the Bonferroni test.

	Topographic formations (n = *10 per position*)				*ANOVA-LMM*
Vegetation variables	*PL*	*SLP*	*FP*	*SGM*	(F, p)
Density					
No. of individuals	22a	22a	30a	4b	2.73*
Richness (*S*)	2.3 ± 0.26a	1.7 ± 0.30a	1.7 ± 0.35a	1.0 ± 0.26b	3.36*
No. of families	4	6	3	2	2.3
No. of genera	4	7	5	2	2.8
No. observed species (% Chao 1)	6 (85.7)	7 (70.0)	6 (85.7)	2 (100)	2.8
No. of estimated species (Chao 1)	7	10	7	2	5.1
Diversity					
Shannon (H') inventory	0.36 ± 0.13	0.35 ± 0.13	0.16 ± 0.14	0.06 ± 0.06	1.6
Simpson (1/D) inventory	1.52 ± 0.19a	1.41 ± 0.26a	1.28 ± 0.24a	0.28 ± 0.20b	7.0**
Margalef (D_{Mg}) inventory	2.1 ± 0.18a	1.4 ± 0.25a	1.4 ± 0.29a	0.4 ± 0.26b	8.2***
Shannon (H') global	1.49	1.46	1.56	0.56	
Simpson (1/*D*) global	3.56	3.14	4.29	1.60	
Cover (%)					
Total vascular plants	38.2 ± 11.8a	23.3 ± 6.5a	43.2 ± 12.9a	2.2 ± 2.0b	3.84*
Bare soil	51.8 ± 10.1a	71.2 ± 6.9a	50.1 ± 14.1a	87.8 ± 3.7b	3.51*

E. interstincta (47.6, 6.0%), *R. exaltata* (43.6, 5.4%), *R. pubera* (30.4, 3.8%), and *S. secans*, *M. reducens*, and *C. alatus*, each with 11.2 (1.4%). Nevertheless, species varied in their ecological representativeness within and among the topographic formations (Table 3). For example, *L. cernua*, *R. tenerrima*, *R. pubera*, and *R. exaltata* had greater representativeness in PL as compared to any other topographic formation, while *E. filiculmis* and *E. interstincta* were dominant in FP. Species such as *C. alatus*, *M. reducens*, and *S. secan* were more relevant in SLP, and *A. bicornis* and *S. bifidus* in SGM. It is worth noting that 45.4% of the identified species were exclusive to a specific topographic formation; for example, *C. alatus*, *M. reducens*, and *S. secans* were found only on SLP, while *E. filiculmis* and *E. interestinta*, having a higher abundance, were only found in PF.

The analysis of floristic similarity using beta-diversity indices (Jaccard and Sørensen indices and their probabilistic estimators) revealed a greater floristic similarity in the species composition of plant communities in PL, SLP, and FP than between these topographic formations and the SGM (Table 4); that is, the number of shared species was higher among PL, SLP, and FP and lower as compared to the SGM.

Relationship Between Topography, Soil Properties, and Vegetation

The PCA revealed a positive relationship between vegetation variables and soil properties (Fig. 4). Density, richness, diversity, and plant cover were positively correlated with soil properties such as silt, clay, OM, calcium, potassium, CEC, and total nitrogen. On the other hand, vegetation variables were negatively related or unrelated to sand (see Table S1). Notably, SGM was associated with sandier soils having the lowest nutrient contents and being devoid of vegetation, whereas the other topographic formations (PL, SLP, and FP) were strongly associated with higher values of vegetation variables and soil properties (Fig. 4).

Discussion

Forest soils impacted by mining experience a decline in fertility (Ramírez-Moreno et al. 2019). In this study, soil fertility in mines was lower than in the reference forests of the same region (see Quinto & Moreno 2014: OM = 5.64 ± 0.1 vs. 7.87 ± 0.1, calcium = 0.30 ± 0.07 vs. 0.34 ± 0.1, magnesium = 0.24 ± 0.1 vs. 0.29 ± 0.1, potassium = 0.23 ± 0.06 vs. 0.21 ± 0.06). Despite the erosion suffered by forest soil when disturbed by mining, the SGM are found to be less fertile than the PL, SLP, and FP. It is likely that SGM are more susceptible to losing nutrients due to water erosion. Chocó is one of the rainiest regions on the globe (up to 13,000 mm/year; Poveda et al. 2004); thus, it is likely that poorer soils in SGM are due to the impact of rainfall (Thompson & Troeh 1982). SGM are rock formations with steep SLP and ample drainage, which favors nutrient washing through rock leaching. Some researchers have found that topographic formations with convex and exposed surfaces (e.g. SGM) facilitate the dragging of smaller particles by runoff (silt, clay, and OM) toward downhill areas, leaving behind the largest particles (e.g. sand and gravel) (Thompson & Troeh 1982). The loss of the soil's organic layer reduces its nitrogen content, and this organic layer may be eroded if factors such as rainfall are high (Thompson & Troeh 1982; Pandey & Singh 1985; Classen & Hogan 2002). Just as topographic formations are disposed of within the mines, soil particles may be disaggregated by rainfall on SGM and deposited in PL and/or in FP. These sites, having a flat and concave shape, respectively, facilitate a greater accumulation of particles from higher topographic positions (Walker & del Moral 2003). For example, Mg^{2+} is a very mobile element in soils because it is less bound to the soil charges. Therefore,

Table 3. Representativeness of the vascular plant species (EII) in the topographic formations of gold mines of Raspadura, Chocó, Colombia. D = density, RD = relative density, F = frequency, RF = relative frequency, EII = Ecological Importance Index.

	Topographic formations (n = *40 plots*)																			
	Plains (n = *10)*					*Slopes* (n = *10)*					*Floodplains* (n = *10)*					*Sand and gravel mounds* (n = *10)*				
Species	D	*RD*	F	*RF*	*EII*	D	*RD*	F	*RF*	*EII*	D	*RD*	F	*RF*	*EII*	D	*RD*	F	*RF*	*EII*
Scleria secans (L.) Urb.						1	4.5	0.1	6.7	11										
Rhynchospora exaltata Kunth	3	13.6	0.3	19	32	1	4.5	0.1	6.7	11										
Lycopodiella cernua (L.) Pic. Serm.	10	45.5	0.6	38	83	11	50	0.4	27	77	6	20	0.4	29	48.6					
Miconia reducens Triana						1	4.5	0.1	6.7	11										
Chelonanthus alatus (Aubl.) Pulle						1	4.5	0.1	6.7	11										
Elecharis filiculmis Kunth											6	20	0.4	29	48.6					
Sticherus bifidus (Willd.) Ching	1	4.5	0.1	6.3	11	2	9.1	0.2	13	22	6	20	0.2	14	34.3	1	25	0.1	33	58.3
Rhynchospora pubera (Vahl) Boeckeler	3	13.6	0.1	6.3	20						1	3.3	0.1	7.1	10.5					
Andropogon bicornis L.	1	4.5	0.1	6.3	11	5	23	0.5	33	56						3	75	0.2	67	141.7
Rynchospora tenerrima Nees ex Spreng.	4	18.2	0.4	25	43						1	3.3	0.1	7.1	10.5					
Elecharis interstincta (Vahl) Roem. & Schult.											10	33	0.2	14	47.6					
Total	22	100	1.6	100	200	22	100	1.5	100	200	30	100	1.4	100	200	4	100	0.3	100	200

Table 4. Floristic similarity among plant communities in the different topographic formations, in gold mines of Raspadura, Chocó, Colombia. J_{abd} and L_{abd} are beta diversity indices of Jaccard and Sorensen based on abundance data and its probabilistic estimates ($\widehat{J}_{abd}$ and $\widehat{L}_{abd}$, respectively).

Topographic formations		*Species richness*			*Abundance-based similarity indices*			
Plant community 1	*Plant community 2*	*Total*	*shared*	*(%)*	J_{abd}	$\hat{J}_{abd}$	L_{abd}	$\widehat{L}_{abd}$
Plains	Slope	9	4	44.4	0.62	0.75	0.76	0.86
Plains	Floodplains	8	4	50.0	0.42	0.56	0.59	0.72
Slope	Sand and gravel mounds	7	2	28.6	0.32	0.35	0.48	0.52
Slope	Floodplains	11	2	18.2	0.31	0.31	0.48	0.48
Floodplains	Sand and gravel mounds	7	1	14.3	0.13	0.15	0.22	0.26
Plains	Sand and gravel mounds	6	2	33.3	0.09	0.11	0.17	0.20

sandy soils with high water conductivity (as observed in SGM) promote Mg^{2+} losses from leaching (Huber & Jones 2013). This may explain the highest Mg^{2+} values in FP recorded in this study.

SGM were the topographic formation displaying the poorest soil fertility and also, the least vegetation. Differences in topography likely result in different conditions of soil fertility that affect early natural revegetation in the mines. Here, plant communities with greater richness, diversity, plant cover, and density were identified in topographic formations where soil nutritional variables attained higher values (e.g. PL, SLP, and FP). This suggests that small spatial variations in the magnitude of soil conditions may have a major influence on early natural mine revegetation (Martínez-Ruiz & Marrs 2007; Sigcha et al. 2018).

PL, SLP, and FP shared more species (floristic similarity) with one another than with mounds of sand and gravel. This may be because, during primary succession, the availability of soil resources for plant survival varies within the system. Therefore, changes in soil conditions may affect plant colonization (Tilman 1985; Walker & del Moral 2003; Walker et al. 2010). The availability of soil nutrients in areas where primary succession is the starting point is considered a limiting factor for the early recovery and natural succession in certain types of plant communities (Tilman 1985; Moreno-de las Heras et al. 2008). For example, Mg^{2+} is an essential mineral contributor to plant health and soil microbial activity (Huber & Jones 2013), explaining why there are higher values of Mg^{2+} in soil and vegetation in FP than in PL, SLP, and SGM. Thus, 45.4% of all species were only present in a specific topographic formation. This supports the idea that mines, despite being systems with less nutrient-rich soil as compared to reference forests, contain a mosaic of soil conditions and the vegetation can grow in these nutrient-deficient soil sites.

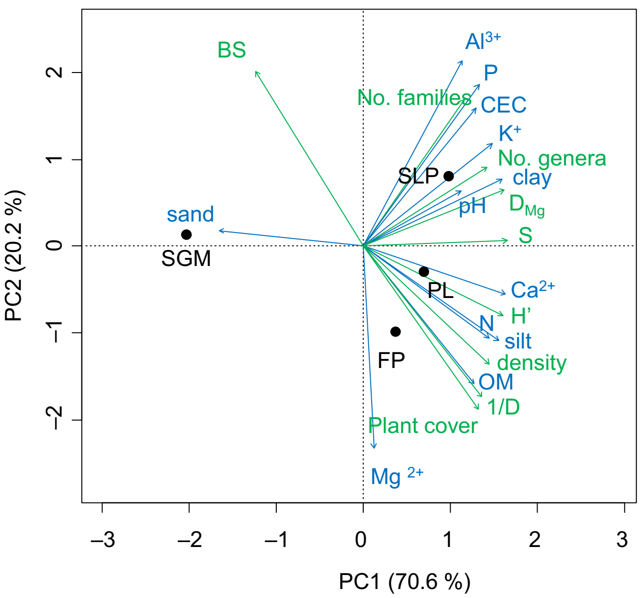

Figure 4. Principal component analysis (PCA) of vegetation variables (green) and soil properties (blue) in the different topographic formations (FP, floodplain; PL, plain; SGM, sand and gravel mounds; SLP, slope) in gold mines of Raspadura, Chocó, Colombia. Abbreviations as in Tables 1 and 2.

Natural plant communities in the different topographic formations were characterized by ruderal native species (except for *Rynchospora exaltata* and *Lycopodiella cernua*; Bernal et al. 2015), but all of the species found (native and non-native) have a wide distribution in the neotropics (http://www.tropicos.org). Unlike the reference forest, much of the mined areas, after years of abandonment, continue to have landscapes with bare soil, grasses, and stagnant waters. This trend of colonization by ruderal plants is typical during the early natural revegetation of gold mines in tropical forests. For example, Valois-Cuesta and Martínez-Ruiz (2017) and Valois-Cuesta et al. (2022) found that, after 24 years of abandonment, gold mines in the rainforests of Chocó (Colombia) were dominated by herbaceous species belonging to the Cyperaceae, Melastomataceae, and Rubiaceae families. Likewise, Chambi-Legoas et al. (2021) determined that pioneer species represented between 50 and 63% of all the species found in plots after 19 years of abandonment in gold mines of the Peruvian Amazon, and Peterson and Heemskerk (2001) noted that a covering of grasses and bare soil dominates in gold mines after 4 years of abandonment in the Suriname Amazon. Thus, natural revegetation in gold mines of tropical forests is slow, given that after 19–24 years of abandonment, the mining areas share less than 8% of their floristic composition with the reference forest (Chambi-Legoas et al. 2021; Valois-Cuesta et al. 2022).

Overall, our results showed that changes in the emergent plant community in abandoned gold mines may be the result of the influence of topographic formations on the spatial distribution of soil fertility. Vegetation is more diverse in topographic formations that are better at promoting the accumulation of soil nutrients (e.g. PL and alluvial plains, and to a lesser degree, SLP), while vegetation is limited in those topographic formations that retain less soil nutrients (SGM). This suggests that the sterile SGM does not promote the early natural revegetation of the abandoned gold mines in the Chocó forests. Our study analyzed the association between topography, soil, and vegetation during early succession (mines with 5 years of natural succession). A more in-depth analysis involved in the dynamics of establishment of native forest species in the topographic formations of abandoned gold mines may be carried out in future studies examining the relationship between topography, soil, and vegetation in longer-term chronosequences (e.g. mines with 10, 20, 30 and greater than 30 years of abandonment).

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LITERATURE CITED

Alvarez-Berríos NL, Aide TM (2015) Global demand for gold is another threat for tropical forests. Environmental Research Letters 10:014006. https://doi.org/10.1088/1748-9326/10/2/029501

Bernal R, Gradstein SR, Celis M (2015) Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. http://catalogoplantasdecolombia.unal.edu.co (accessed 13 Feb 2014)

Bradshaw AD (1984) Ecological principles and land reclamation practice. Landscape Planning 11:35–48. https://doi.org/10.1016/0304-3924(84)90016-9.

Bradshaw AD (1997) Restoration of mined land—using natural processes. Ecological Engineering 8:255–269. https://doi.org/10.1016/S0925-8574(97)00022-0

Chambi-Legoas R, Ortega Figueiredo DR, De Marques F, Peña J, Zevallos PA, Marcelo-Pena JL, Rother DC (2021) Natural regeneration after gold mining in the Peruvian Amazon: implications for restoration of tropical forests. Frontiers in Forests and Global Change 4:594627. https://doi.org/10.3389/ffgc.2021.594627

Chao A, Chazdon R, Colwell RK, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8:148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Chase MW, Reveal JL (2009) A phylogenetic classification of the land plant to accompany APG III. Botanical Journal of the Linnean Society 161:122–127. https://doi.org/10.1111/j.1095-8339.2009.01002.x

Classen VP, Hogan MP (2002) Soil nitrogen pool associated wind revegetation of disturbed sites in the Lake Tahoe area. Restoration Ecology 10:195–203. https://doi.org/10.1046/j.1526-100X.2002.00228.x

Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples, version 9. http://purl.oclc.org/estimates (accessed 2 Sep 2022)

Ellery KS, Walker BH (1986) Growth characteristics of selected plant species on asbestos tailing from Msauli Mine, eastern Transvaal. South African Journal of Botany 52:201–206. https://doi.org/10.1016/S0254-6299(16)31550-2

Gentry AH (1996) A field guide to the families and genera of woody plants of north west South America (Colombia, Ecuador, Perú): with supplementary notes on herbaceous taxa. Conservation International, Washington, D.C.

Haston E, Richardson JE, Stevens PF, Chase MW, Harris DJ (2009) The linear angiosperm phylogeny group (LAPG) III: a linear sequence of the families in APG III. Botanical Journal of the Linnean Society 161:128–131. https://doi.org/10.1111/j.1095-8339.2009.01000.x

Hobbs RJ, Norton DA (1996) Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93–110. https://doi.org/10.1111/j.1526-100X.1996.tb00112.x

Hoogendoorn CJ, Newton PCD, Devantier BP, Rolle BA, Theobald PW, Lloyd-West CM (2016) Grazing intensity and micro-topographical effects on some nitrogen and carbon pools and fluxes in sheep-grazed hill country in New Zealand. Agriculture, Ecosystems and Environment 217:22–32. https://doi.org/10.1016/j.agee.2015.10.021

Huber DM, Jones JB (2013) The role of magnesium in plant disease. Plant and Soil 368:73–85. https://doi.org/10.1007/s11104-012-1476-0

Kumhálová J, Kumhála F, Kroulík M, Matějková Š (2011) The impact of topography on soil properties and yield and the effects of weather conditions. Precision Agriculture 12:813–830. https://doi.org/10.1007/s11119-011-9221-x

López-Marcos D, Turrión MB, Martínez-Ruiz C (2020) Linking soil variability with plant community composition along a mine-slope topographic gradient: implications for restoration. Ambio 49:337–349. https://doi.org/10.1007/s13280-019-01193-y

Martínez-Ruiz C, Fernández-Santos B, Gómez-Gutiérrez JM (2001) Effects of substrate coarseness and exposure on plant succession in uranium-mining wastes. Plant Ecology 155:79–89. https://doi.org/10.1023/A:1013208305393

Martínez-Ruiz C, Marrs RH (2007) Some factors affecting successional change on uranium mine wastes: insights for ecological restoration. Applied Vegetation Science 10:333–342. https://doi.org/10.1111/j.1654-109X.2007.tb00432.x

Martins WBR, Rodrigues JLM, de Oliveira VP, Ribeiro SS, Barros WS, Schwartz G (2022) Mining in the Amazon: importance, impacts, and challenges to restore degraded ecosystems. Are we on the right way? Ecological Engineering 174:106468. https://doi.org/10.1016/j.ecoleng.2021.106468

Moreno-de las Heras M, Nicolau JM, Espigares T (2008) Vegetation succession in reclaimed coalmining slopes in a Mediterranean-dry environment. Ecological Engineering 34:168–178. https://doi.org/10.1016/j.ecoleng.2008.07.017

Murcia C, Guariguata MR (2014) La restauración ecológica en Colombia: tendencias, necesidades y oportunidades (Documentos Ocasionales 107). CIFOR, Bogor, Indonesia. https://doi.org/10.17528/cifor/004519

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2020) Vegan: community ecology package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan (accessed 9 May 2022)

Pandey AN, Singh JS (1985) Mechanism of ecosystem recovery: a case study from Kumaun Himalaya. Recreation and Revegetation Research 3:271–292. https://api.semanticscholar.org/CorpusID:130825297

Pastorok RA, MacDonald A, Sampson JR, Wilber P, Yozzo DJ, Titre JP (1997) An ecological decision framework for environmental restoration projects. Ecological Engineering 9:89–107. https://doi.org/10.1016/S0925-8574(97)00036-0

Pérez-Escobar OA, Lucas E, Jaramillo C, Monro A, Morris SK, Bogarín D, et al. (2019) The origin and diversification of the hyperdiverse flora in the Chocó biogeographic region. Frontiers in Plant Science 10:1328. https://doi.org/10.3389/fpls.2019.01328

Peterson GD, Heemskerk M (2001) Deforestation and forest regeneration following small-scale gold mining in the Amazon: the case of Suriname. Environmental Conservation 28:117–126. https://doi.org/10.1017/S0376892901000121

Pinheiro JC, Bates DM (2000) Linear mixed-effects models: basic concepts and examples. In: Mixed-effects models in S and S-PLUS. Springer, New York

Pinheiro J, Bates D, DebRoy S, Sarkar D, R-Core Team (2021) Nlme: linear and nonlinear mixed effects models. R package version 3.1-152.

Poveda MC, Rojas PCA, Rudas LIA, Rangel-Churio JO (2004) El Chocó biogeográfico: ambiente físico. Pages 1–22. In: Rangel-Churio JO (ed) Colombia diversidad biótica IV, El Chocó biogeográfico/Costa Pacífica. Universidad Nacional de Colombia-Conservación Internacional, Bogotá, Colombia

Quinto H, Moreno F (2014) Diversidad florística arbórea y su relación con el suelo en un bosque pluvial tropical del Chocó biogeográfico. Árvore 38:1123–1132. https://doi.org/10.1590/S0100-67622014000600017

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramírez A (2006) Ecología, métodos de muestreo y análisis de poblaciones y comunidades. Pontificia Universidad Javeriana, Bogotá, Colombia

Ramírez-Moreno G, Quinto H, Vargas L, Orlando J, Rangel JO (2019) Temporary effect of mining on breathing and on the physicochemical conditions of soil. Modern Environmental Science and Engineering 837:837–848. https://doi.org/10.15341/mese(2333-2581)/09.05.2019/007

Rangel-Churio JO (2004) Colombia diversidad biótica IV – El Chocó biogeográfico/Costa Pacífica. Universidad Nacional de Colombia-Conservación Internacional, Bogotá, Colombia

Rangel-Churio JO, Rivera-Díaz O (2004) Diversidad y riqueza de espermatofitos en el Chocó biogeográfico. Pages 83–104. In: Rangel-Churio JO (ed) Colombia diversidad biótica IV, El Chocó biogeográfico/Costa Pacífica. Universidad Nacional de Colombia-Conservación Internacional, Bogotá, Colombia

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86:2805–2814. https://doi.org/10.1890/05-0074

Román-Dañobeytia F, Cabanillas F, Lefebvre D, Farfan J, Alferez J, Polo-Villanueva F, et al. (2021) Survival and early growth of 51 tropical tree species in areas degraded by artisanal gold mining in the Peruvian Amazon. Ecological Engineering 159:106097. https://doi.org/10.1016/j.ecoleng.2020.106097

Sigcha F, Pallavicini Y, Camino MJ, Martínez-Ruiz C (2018) Effects of short-term grazing exclusion on vegetation and soil in early succession of a subhumid Mediterranean reclaimed coal mine. Plant and Soil 426:197–209. https://doi.org/10.1007/s11104-018-3629-2

Siqueira-Gay J, Sánchez LE (2021) The outbreak of illegal gold mining in the Brazilian Amazon boosts deforestation. Regional Environmental Change 21:1–5. https://doi.org/10.1007/s10113-021-01761-7

Sokal RR, Rohlf FJ (1995) Biometry. 3rd ed. W.H. Freeman and Co., New York

Thompson LM, Troeh FR (1982) Los suelos y su fertilidad. Reverte S.A., Barcelona, Spain

Tilman D (1985) The resource-ratio hypothesis of plant succession. The American Naturalist 123:827–852. https://doi.org/10.1086/284382

Valois-Cuesta H, Martínez-Ruiz C (2016) Vulnerability of native forests in the Colombian Chocó: mining and biodiversity conservation. Bosque (Valdivia) 37:295–305. https://doi.org/10.4067/S0717-92002016000200008

Valois-Cuesta H, Martínez-Ruiz C (2017) Colonizer plant species of sites disturbed by mining in the Chocoan rain forest, Colombia. Biota Colombiana 18:88–104. https://doi.org/10.21068/c2017.v18n01a7

Valois-Cuesta H, Martínez-Ruiz C, Quinto-Mosquera H (2022) Natural revegetation of areas impacted by gold mining in the tropical rain forest of Chocó, Colombia. Revista de Biología Tropical 70:e50653. https://doi.org/10.15517/rev.biol.trop..v70i1.50653

Villareal H, Álvarez M, Córdoba S, Escobar F, Fagua G, Gast F, Umaña AM (2006) Manual de métodos para el desarrollo de inventarios de biodiversidad. 2nd ed. Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Bogotá, Colombia

Walker LR, del Moral R (2003) Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge, United Kingdom. https://doi.org/10.1017/CBO9780511615078

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x

Supporting Information

The following information may be found in the online version of this article:

Table S1. Relationship (Pearson correlation coefficient) between vegetation variables and soil physical and chemical properties in gold mines of Raspadura, Chocó, Colombia.

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