Research article

Changes in floristic and vegetation structure in a chronosequence of abandoned gold-mining lands in a tropical Amazon forest

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ABSTRACT

This study analyzes floristic and vegetation structure changes during forest succession after disturbances caused by small-scale gold mining in Madre de Dios (Peru). We compared the floristic and vegetation structure of a reference forest against three sites with different periods of abandonment after mining (5, 11 and 23-years). Three 20×60 m plots were defined on each site, and all tree species with a DBH >1 cm within the plots were inventoried. To evaluate species diversity and similarity, the Importance Value, effective numbers of species (^{0}D, ^{1}D, and ^{2}D), and Chao-Jaccard similarity index were calculated. We used the Nonmetric multidimensional scaling for similarity ordination and the PERMANOVA test to evaluate differences in floristic composition. We recorded 129 tree species in the study areas and statistically significant differences between initial and intermediate stages were observed regarding floristic composition, basal area, height, and DBH. The transition from the initial successional stage to the reference forest produces an increase in basal area, species diversity, and floristic similarity. The 23-year-old stand had more species in common with the 11-year-old stand than the reference forest. Our results showed a high proportion of pioneer species and anemochory dispersal syndrome in the initial successional stages, but they decreased in later stages of the chronosequence. The floristic and structural attributes of forests throughout the chronosequence showed a fast recovery during secondary succession. After 23 years, the recovery of tree species density was 77 % of reference forest, while the relative recovery of species composition was much slower, on average 23 %. These results provide essential information to guide the selection of suitable species in ecological restoration projects after abandonment. Implementing forest restoration strategies based on reliable information to accelerate the process of vegetation succession is critical for recuperating areas degraded by gold mining at the Peruvian Amazon.

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1. Introduction

Mining is a crucial activity in the global economy and the development of many societies [1,2]. It affects most ecosystems and is considered the most destructive anthropogenic activity [3]. Artisanal and small-scale gold mining (ASGM) is widespread worldwide, especially in developing countries [1], where it is an essential part of the local economy. Although mining activities occur on a small part of the land surface (less than 1 %) [1] they cause severe impacts and environmental degradation [4,5], with potentially profound
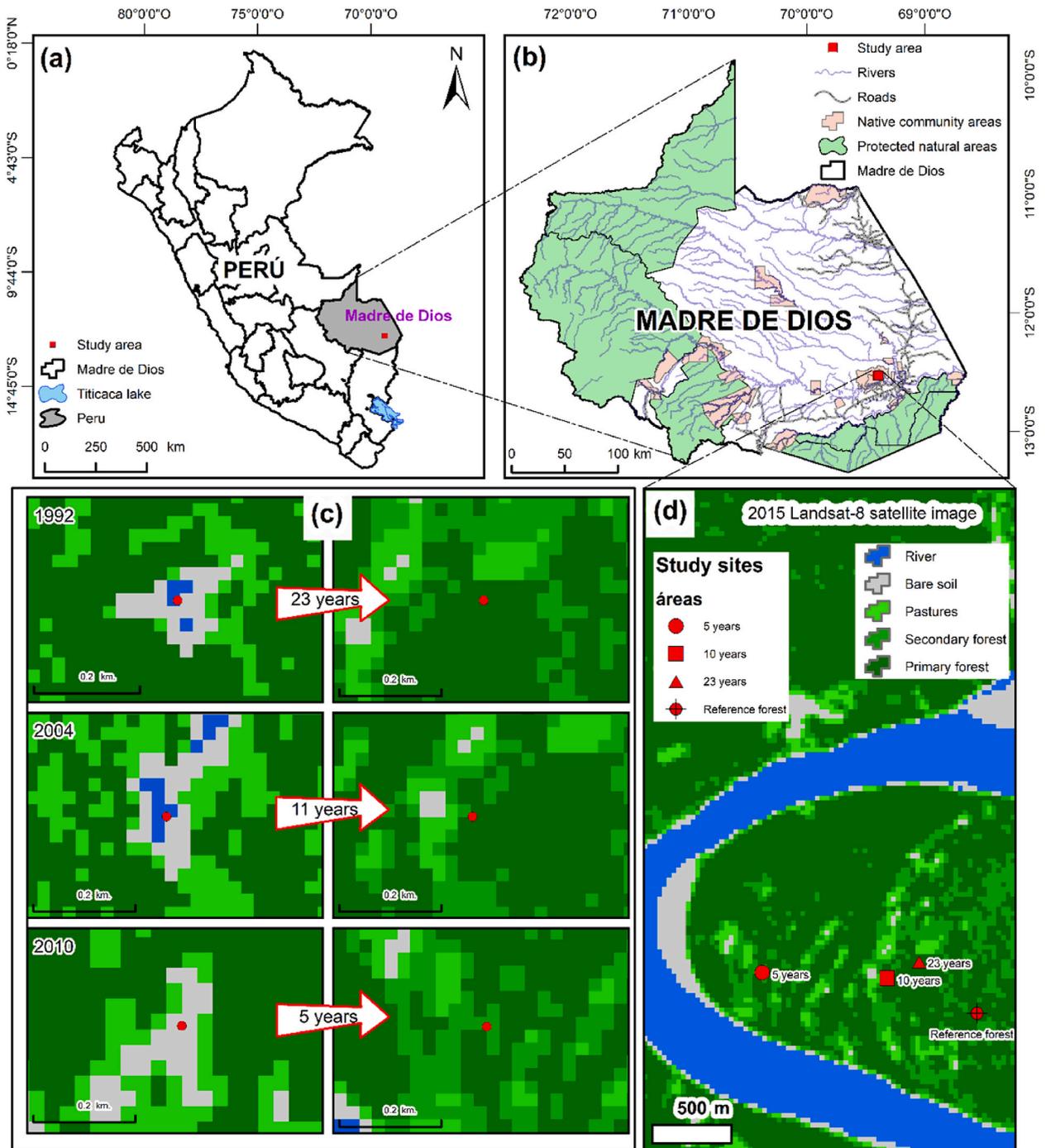
Fig. 1. The geographic location of studied sites and matrix configuration surrounding each stand at Tres Islas indigenous community (Madre de Dios), southeastern Peru. (a) Map of Perú showing Madre de Dios region (b). (c and d) Map of the location of four study sites, three from different periods since gold mining was abandoned and the reference forest.

effects on the health of local populations [6].

Madre de Dios "the capital of biodiversity" encompasses one of Amazonia's most diverse and best-preserved forest areas [7]. However, this mega-diversity is also threatened by extractive activities such as ASGM. Gold-mining in Madre de Dios causes negative impacts on human health due to mercury release into the atmosphere, rivers and soils [7–9]. It also removes all aboveground vegetation, and seriously degrades the soil [2,10,11]. Consequently, due to severe impacts on soil quality (structure and chemical properties) [12], mining may limit forest recovery [5]. A recent study reported that 95,000 ha of Madre de Dios primary forests were destroyed due to gold-mining activities in the last 34 years [13] even though gold-mining activities have occurred in Madre de Dios since colonial times [6].

Ecological restoration is "the process of assisting the recovery of a degraded, damaged, or destroyed ecosystem to reflect values regarded as inherent in the ecosystem and to provide goods and services that people value" [14]. A key nature-based solution to halt and reverse biodiversity loss, mitigate climate change, and provide direct socioeconomic benefits is the restoration of tropical forests through tree planting that promotes ecosystem recovery [15]. Active restoration methods like direct seeding or nursery-raised seedlings are used when natural regeneration is impossible [16], with the latter being the most widely used to recover degraded areas by gold mining in Madre de Dios [17–20]. Even though passive restoration is possible when the degraded ecosystem has some resilience and no strong biotic or abiotic filters that limit the establishment of natural regeneration [16]. In this context, several studies have been reported a slow recovery of tree vegetation in degraded lands abandoned by gold-mining in Madre de Dios [21,22]. This is why some active restoration strategies are needed to accelerate forest recovery.

Chronosequence studies are the most commonly used approaches in research on tropical forest succession [23]. Chronosequence involve a set of observations that occur under similar climatic, environmental, and edaphic conditions but differ in terms of vegetation age [11]. Chronosequence studies are common because they provide immediate results for minimal effort and significantly extend the potential time of a study [2]. There are many chronosequence studies about secondary succession on abandoned tropical fields, e.g., after pasture or agriculture [23–26]. There are many studies of natural vegetation recovery in the Brazilian Amazon after mining [5, 27–29]. However, few studies have been done on vegetation recovery in abandoned gold mining lands in the southeastern Peruvian Amazon. Studies that compare successional stages throughout a chronosequence with a mature reference forest are scarce. We consider the study of secondary succession in abandoned areas after gold-mining in Madre de Dios to be a key for forest recovery efforts because the effects of that disturbance are severe, and all vestiges of biological activity and propagules in the soil are removed [2,4].

In this study, we conducted the first comparison between multiple stages of vegetation succession after gold mining and a reference forest in the southeastern Peruvian Amazon. We address the following research questions: (1) Does the similarity in species composition to the reference forest increase with time along the chronosequence of 23-year-old stands after abandonment by gold-mining activities? (2) How do the forest's structural attributes change during a period of 23 years after abandonment? (3) How do successional categories and dispersal syndromes change along the successional chronosequence? We anticipate that answers to these questions may be essential in designing vegetation recovery practices for the Amazon forests.

2. Materials and methods

2.1. Study area

The study was carried out in abandoned areas after gold mining (central location: 12° 31′ 34.22″ S and 69°23' 45.77" W) in Tres Islas indigenous community, Madre de Dios region, in southeastern Peru (Fig. 1). This site is located 27 km northeast of the town of Puerto Maldonado. Mean annual temperature and mean annual rainfall (for 1980–2016) are 25.4 °C and 2120 mm, respectively, with a dry season from June to September when the rainfall is less than 100 mm per month (Fig. S1).

The study area is a mosaic of vegetation that stands at different succession stages after the abandonment of small-scale gold-mining activities. Miners used an open-pit mining process to obtain gold. The usual size of small-scale mining operations is 1–3 ha. In such operations, all aboveground vegetation must be cut, and the soil is completely removed. Then, during dredging operations, gold-containing soils are pumped from the deep pits (up to 10 m) to a sluice box, which collects gold particles. The mines in the Tres Islas indigenous community have a dispersed spatial pattern, such that the mining pits are surrounded by forest fragments.

2.2. Study design

We evaluated the floristic composition and vegetation structure of the reference forest, a significant benchmark, and three zones with different periods since gold mining was abandoned, up to 23 years. Three forest stands in different successional stages after gold mining were selected to establish a chronosequence. The chronosequence included initial succession (5-years), intermediate (11 years) and later stages (23 years) [30]. An old-growth forest (reference forest) affected by selective logging of low intensity was selected to compare with the successional forest regarding changes in species richness and structural attributes in the chronosequence. We selected this forest because it is close to the stands and represents the typical forests of Madre de Dios.

The time since the abandonment of gold-mining fields and sampling plot locations were determined using Landsat images (1975–2014) and the software CLASlite [31]. This information was complemented with interviews with the local population (January 2015) and a review and evaluation of the soil to verify that it had evidence of the impact of mining activities. Thus, we could confirm that the three selected stands of 5, 11, and 23 years were abandoned in 2010, 2004, and 1992, respectively. The three chosen stands were located next to the reference forest, and the distance between the stands and the reference forest was similar and small (from 50 m to 80 m).

2.3. Data collection

For each stand, vegetation was sampled in three plots of 20 m × 60 m (0.12 ha), divided into three 20 m × 20 m sub-plots where all individuals with a stem diameter at breast height (DBH) greater than 1 cm were inventoried. The woody vegetation was classified according to the stage of development of the individuals [32], classified as saplings (1 cm to < 5 cm DBH), poles (5 cm to < 10 cm DBH) and mature trees (>10 cm DBH). Total height (TH) and DBH of all individuals were measured, and botanical samples were collected and deposited for identification in the Alwyn Gentry herbarium (HAG) at the Universidad Nacional Amazónica de Madre de Dios. The genera and families were classified according to the Angiosperm Phylogeny Group (APG IV) [33]. The scientific names, genera, and families were standardized by cross-checking with the Taxonomic Name Resolution Service app (https://tnrs.biendata.org/) [34].

2.4. Data analysis

To evaluate changes in vegetation diversity, we calculated species density, and the total number of individuals, genera, and families. We used effective numbers of species or Hill numbers (^0D, ^1D, and ^2D) to quantify species diversity of forest through the chronosequence. Hill numbers are a mathematically unified family of diversity indices incorporating relative abundance and species richness [35]. The calculations were performed using the hillR package of R software [36] for the three components of species diversity represented by the Hill series cc (^0D, species richness weighting all species equally; ^1D, exponential of Shannon's entropy index weighting typical species; ^2D, inverse of Simpson's concentration index weighting dominant species). Forest structure was analyzed by size and demographic structure using tree DBH 10-cm classes. The number of individuals and the mean tree height were calculated for each DBH class.

To evaluate changes in abundance and dominance of species and families, we compared the importance values in the stands for families (FIV) and species (IV) across the successional stages. The IV simplifies the Importance Value Index (IVI) proposed by Curtis & McIntosh [37] where frequency is ignored. According to Lozada [38], the IV has the same advantages of IVI, and it is more suitable in small plots. Significant differences between forests were evaluated using ANOVA and the Student-Newman-Keuls *post-hoc* test (SNK) at the 5 % significance level. Before performing the ANOVA test, its assumptions were verified. We used the Shapiro Wilk test for normality and the Levene test for homoscedasticity. Indicator species analysis (IndVal) was used to find indicator species and species assemblages that characterize groups throughout the chronosequence and reference forest [39]. The species indicator analysis (IndVal) was conducted using the Multipatt function of indicspecies R package [40]. This analysis was performed for each development stage of the individuals (saplings, poles and mature trees). Species with an IndVal statistic value higher than 70 % and a $p < 0.05$ were considered indicator species for each successional stage in the chronosequence and reference forest.

To examine patterns and similarities in floristic composition throughout the chronosequence, we used nonmetric multidimensional scaling (NMDS). NMDS was performed using a species abundance matrix (DBH >1 cm) and Chao-Jaccard distance. We used a square root transformation to lower the influence of dominant species on the NMDS [41]. The calculations were performed using the CommEcol R library [42], and the NMDS plot was performed using the PRIMER 7 software [43]. To evaluate relationships among NMDS axes, we analyzed floristics and structural variables of the stands using Spearman correlations.

To evaluate the significance of differences in tree species composition among the three successional stands and reference forest, we used a permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA and *a posteriori* pair-wise comparison analyses were performed in PRIMER 7 with the PERMANOVA + add-on [43], with a significance level of 1 %. In all analyses, 9999 permutations were run.

Species found were classified in successional categories according to Gandolfi et al. [44]. Pioneer, early secondary, late secondary, and undetermined were grouped in the "unclassified" category. Shade-tolerant species were classified as late secondary, while shade-intolerant species were classified as pioneer [28,44]. To analyze the dispersal syndrome, all species with a DBH >1 cm were classified according to Schulze et al. [45] into: zoochory (dispersal by animals), anemochory (dispersal by wind), and autochory (self-dispersal). To evaluate changes in successional categories and dispersal syndromes, we calculated the proportion of species in each one and compared the findings across the chronosequence.

Table 1

Diversity and structure (±SD) results for three forest stands with different periods of time after mining and reference forest (DBH >1 cm). Means followed by the same letter do not differ significantly ($p > 0.05$).

Time since abandonment	No. of Genera	No. of Families	Basal area (m^2/ ha)	Density (N/0.12 ha)	Species density (^0D)	Hill number (^1D)	Hill number (^2D)
5-years	28	17	2.38 ± 0.12 d	352 ± 22.54 a	25 ± 3.46 c	11.74 ± 0.94 d	7.85 ± 0.47 c
11-years	43	24	3.75 ± 0.34 c	267 ± 2 b	46 ± 1.73 b	19.74 ± 1.87 c	10.47 ± 1.61 c
23-years	47	27	5.24 ± 0.38 b	213.67 ± 37.10 c	49.67 ± 1.53 b	31.07 ± 0.83 b	18.62 ± 2.40 b
Reference forest	57	31	13.32 ± 3.09 a	292.67 ± 17.01 b	65.65 ± 0.58 a	51.74 ± 1.11 a	41.83 ± 1.04 a

3. Results

3.1. Changes in diversity, floristics and forest structure

We recorded 129 tree species (Table S1). Comparing across stands, the number of genera and families increased with time since abandonment. The number of genera rose from 28 in the 5-year-old stand to 47 in the 23-year-old stand. Similarly, the number of families increased from 17 in the 5-year-old stand to 27 in the 23-year-old stand. This values are all lower than those in the reference forest (Table 1).

Mean species density, basal area, and effective numbers of species also increase with stand age. Differences between the three successional stands and the reference forest were statistically significant (Table 1). However, mean species density did not differ significantly ($p > 0.05$) between 11 years and 23 years after abandonment (Table 1). Diversity was lowest in the 5-year-old stand due to high densities of *Cecropia membranacea, Inga marginata, Tessaria integrifolia, Senegalia polyphylla,* and *Trema micrantha.* The five species represent 70 % of all individuals larger than 1 cm DBH and 72 % of all tree individuals (DBH >10 cm). The mean basal area of the reference forest was 13 m^2/ha, two and a half times higher than the mean of the 23-year-old stand, 5.2 m^2/ha.

Tree density throughout the chronosequence was unrelated to time since abandonment because mean density did not differ significantly between the reference forest and the 11-year-old stand (Table 1). However, basal areas differ significantly among stands, and the lowest values occur in the initial stages and the highest in the reference forest (Table 1). On the other hand, mean species density and diversity increased with increasing abandonment age, reaching a peak in the 23-year-old-stand (Table 2). We found changes in species density and diversity patterns among the tree size categories across chronosequence stages and the reference forest (Table 2). In saplings, poles, and mature trees, we found significant differences in mean species density and diversity among the three successional stands and the reference forest ($p < 0.05$). In poles and saplings, mean species density did not differ significantly ($p > 0.05$) among those aged 5, 11, and 23 years after abandonment (Table 2). However, in mature trees, the mean species density of 11, and 23 years-old-stands were significantly higher than 5 years-old-stand ($p < 0.05$). Stands in the mature trees and poles only recovered 45–49 % of the species found in the reference forest, whereas saplings had the highest proportion of species numbers (between 65 and 74 %) (Table 2).

The higher density of small individuals (DBH <10 cm) in comparison with mature ones indicates an inverted J-shaped frequency distribution for the successional stands and reference forest (Fig. 2). In the 5- and 11-year-old stands, tree density in the smallest DBH classes (<10 cm) represented more than 76 % of recorded individuals. However, considering DBH classes less than 20 cm, relative tree density decreased with time since abandonment and was the lowest in the reference forest.

Mean total height increases with time since abandonment (Fig. 2a, b, c). DBH classes have increased since abandonment, from four in the 5-year-old stand to 11 in the reference forest. In the 5-year-old stand, we did not find trees ≥40 cm DBH. The average total height (TH) for the largest DBH category was 11.7 ± 4.1 m, while taller species were *C. membranacea, I. marginata,* and *Sapium marmieri* (TH > 10 m). In the 11-year-old stand, unexpectedly, we found a few trees in the 50–80 cm DBH class (4 trees of *Ficus insipida*). Average TH for the 40–50 cm diametric category was 16.75 ± 2.3 m, while taller species were *F. insipida, C. membranacea,* and *Ochroma pyramidale* (TH > 14 m). In the 23-year-old stand, we did not find trees ≥60 cm DBH. The average TH for the biggest DBH category (50–60 cm) was 24.7 ± 1.9 m, while the tallest species were *S. polyphylla, S. marmieri, Guazuma crinita* and *Coccoloba williamsii* (TH > 21 m).

The most important tree species in the 5-year-old stand was *I. marginata* (IV = 24.3 %), followed by typical pioneer species such as *C. membranacea* (24.3 %), *T. micrantha* (6.6 %), *T. integrifolia* (3.9 %), and *O. pyramidale* (3 %) (Table 3). In the 11-year-old stand, the early secondary species *F. insipida* (23.9 %) and *Inga sertulifera* (12.9 %) were the most important, followed by pioneer tree species *C. membranacea* (11.1 %) and *O. pyramidale* (4.5 %). In the 23-year-old stand, the late secondary species *S. marmieri* (32.8 %) was the most important, followed by early secondary species *Pourouma cecropiifolia* (9.3 %) and *Annona pittieri* (3.2 %). However, we found few pioneer tree species in the advanced successional stage, such as *S. polyphylla* (6.3 %) and *G. crinita* (5.5 %) (Table 3 and Table S1).

Table 2
Species richness and diversity (±SD) by development stage for three forest stands with different periods of time after mining and reference forest (DBH >1 cm). Means followed by the same letter do not differ significantly ($p > 0.05$).

Development stage/Stand	Total of species	Species density (^{0}D)	Hill number (^{1}D)	Hill number (^{2}D)
Mature Trees				
Reference forest	64	48.33 ± 4.16 a	39.51 ± 5.28 a	32.07 ± 5.99 a
23-years	28	23.67 ± 2.08 b	13.61 ± 0.69 b	7.83 ± 0.79 b
11-years	29	21.67 ± 1.15 b	13.59 ± 2.37 b	9.70 ± 2.2 b
5-years	21	15.67 ± 4.16 c	8.62 ± 2.50 b	5.88 ± 1.91 b
Poles				
Reference forest	63	51.33 ± 4.51 a	42.08 ± 3.96 a	34.94 ± 3.70 a
23-years	31	25.33 ± 4.04 b	19.58 ± 1.67 b	15.84 ± 0.88 c
11-years	32	24.67 ± 3.51 b	11.81 ± 1.88 c	21.73 ± 3.61 b
5-years	24	18.33 ± 3.06 b	9.39 ± 1.09 c	6.88 ± 0.62 d
Saplings				
Reference forest	59	39.67 ± 3.51 a	34.67 ± 0.95 a	30.07 ± 2.75 a
23-years	34	26.00 ± 1.73 b	22.05 ± 1.40 b	18.67 ± 0.67 b
11-years	42	29.33 ± 5.13 b	15.89 ± 1.40 c	9.68 ± 0.67 c
5-years	25	18.33 ± 4.93 b	11.12 ± 1.15 d	8.51 ± 0.06 c
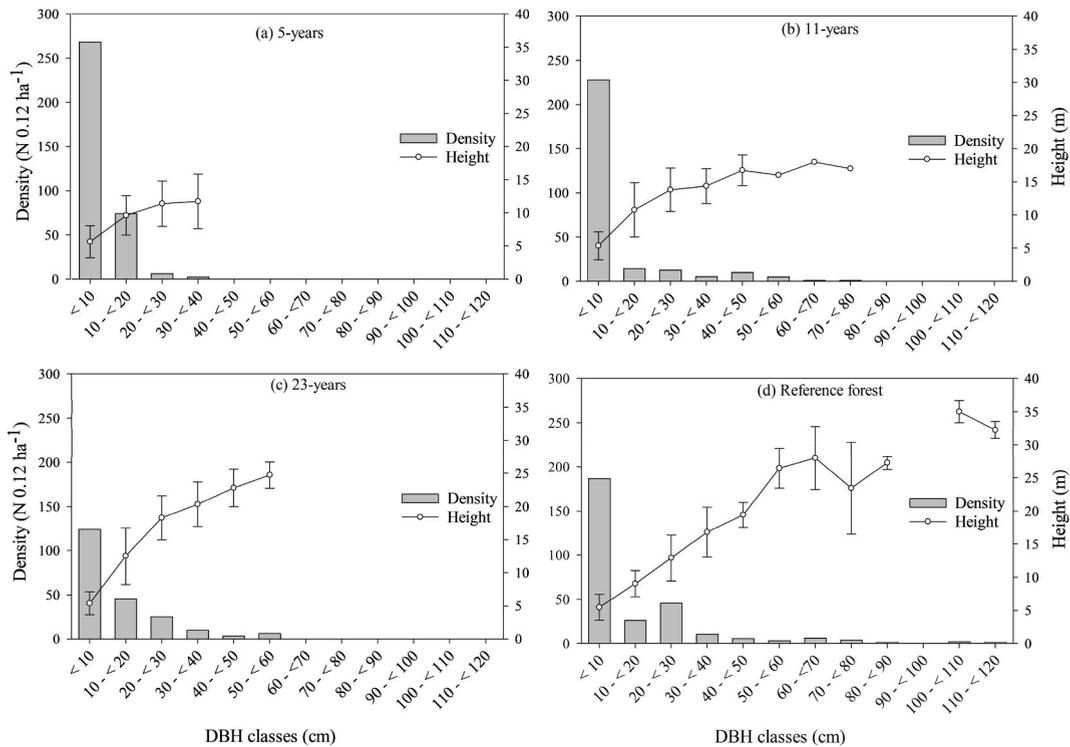
Fig. 2. Tree density and mean total height (±SD) by DBH classes (10-cm interval) for three stands with different periods of time after mining and reference forest (DBH >1 cm).

For the poles category, the most important species in the 5-year-old stand were pioneer tree species *C. membranacea* (22.4 %), *T. integrifolia* (21.1 %), *O. pyramidale* (2.7 %), and *T. micrantha* (2.6 %). In the 11-year-old stand, the early secondary species *I. sertulifera* (34.6 %), *Margaritaria nobilis* (14.2 %), and *F. insipida* (6.3 %) were the most important, followed by a few pioneer tree species as *C. membranacea* (3.8 %) and *Croton lechleri* (2.4 %). In the 23-year-old stand, early secondary species *C. williamsii* (15.9 %) and *Tabernaemontana sananho* (8.4 %) were the most important, followed by common late secondary species *Virola calophylla* (8 %), *Guarea macrophylla* Vahl (4.6 %), *Gallesia integrifolia* (4.4 %), and *Trichilia maynasiana* (4.1 %). Interestingly, in the pole category, we did not find pioneer tree species in the 23-year-old stand (Table 3).

For the saplings category, the most important species in the 5-year-old stand were pioneer species *T. integrifolia* (17.5 %), *C. membranacea* (17.1 %), and *S. polyphylla* (9.5 %), followed by a few intermediate succession species *I. marginata* (16.8 %), *Senna herzogii* (6.6 %), and *Acalypha mapirensis* (5.8 %). Among the ten most important species in the 5-year-old stand, only one late secondary species, *M. nobilis* was recorded (5.6 %). In the 11 and 23-year-old stands, early and late secondary species were the most important (Table 3).

Few species were dominant in the stands studied, and their dominance decreased during succession. The ten most important tree species decreased from 86.8 % in the 5-year-old stand to 78.8 % of IV in the 23-year-old stand, which in turn was higher than in the reference forest (43.3 % IV). Likewise, the ten most important pole species decreased from 88.8 % in the 5-year-old stand to 70 % of IV in the 23-year-old stand, which in turn was higher than in the reference forest (36.9 % IV). Similarly, the ten most important sapling species decreased from 87.2 % in the 5-year-old stand to 56.3 % of IV in the 23-year-old stand, which was higher than in the reference forest (36 % IV).

Fabaceae, Urticaceae, Moraceae and Asteraceae were the most abundant and dominant families in the initial successional stage (Table S2). In the 11-year-old stand, Fabaceae, Moraceae, and Urticaceae were the most abundant and dominant families. However, in the 23-year-old stand, Euphorbiaceae and Fabaceae were the most abundant and dominant families (Table S2). Urticaceae and Asteraceae were important for the initial successional stages, though their abundance and dominance decreased with time since abandonment.

IndVal analysis show that indicator species increased across the chronosequence. This IndVal pattern varies according to stage of development (Fig. 3). *O. pyramidale*, *S. humboldtiana* and *T. micrantha* were found as indicators of poles and mature trees in the 5-year-old stand. This suggests that *O. pyramidale*, *S. humboldtiana* and *T. micrantha* generate favorable conditions for the establishment of early and late secondary species [46,47]. Among saplings, we found other indicator species, including pioneers such as *C. laevigata*, *C. membranacea* and *T. integrifolia*, as well as species from early successional stages, such as *S. parahyba*, *M. lanceolata,* and *H. acuminata* (Fig. 3). Comparing all species recorded, 62 were strongly associated with only one of the stands or reference forest (IndVal >0.70; *p* < 0.05). Six species were found to be indicators of the 5-year-old, 12 of the 11-year-old stand, and 15 of the 23-year-old stand, with 26 in

Table 3

Species with the highest Importance index (% IV) by development stage for three forest stands with different periods of time after mining and reference forest.

Growing stage	N	5-years Species	% IV	11-years Species	% IV	23-years Species	% IV	Reference forest Species	% IV
Saplings	1	*Tessaria integrifolia*	17.5	*Margaritaria nobilis*	21.6	*Sapium marmieri*	9.3	*Leonia crassa*	5.7
	2	*Cecropia membranacea*	17.1	*Inga sertulifera*	18.5	*Miconia affinis*	8.8	*Gallesia integrifolia*	4.4
	3	*Inga marginata*	16.8	*Guatteria scytophylla*	7.7	*Guazuma crinita*	7.3	*Nectandra olida*	4.0
	4	*Senegalia polyphylla*	9.5	*Miconia trinervia*	7.5	*Leonia crassa*	5.4	*Tabernaemontana sananho*	3.5
	5	*Senna herzogii*	6.6	*Inga marginata*	5.1	*Pleurothyrium bifidum*	4.7	*Virola surinamensis*	3.4
	6	*Acalypha mapirensis*	5.8	*Inga heterophylla*	2.6	*Coccoloba williamsii*	4.7	*Lonchocarpus guillemineanus*	3.1
	7	*Margaritaria nobilis*	5.6	*Calycophyllum spruceanum*	2.5	*Lacistema aggregatum*	4.6	*Ficus pallida*	3.1
	8	*Trema micrantha*	4.1	*Coccoloba williamsii*	2.4	*Guazuma ulmifolia*	4.0	*Guarea macrophylla*	3.0
	9	*Inga sertulifera*	2.3	*Palicourea sp1*	2.3	*Gallesia integrifolia*	4.0	*Psychotria racemosa*	2.9
	10	*Croton lechleri*	1.8	*Sapium glandulosum*	2.2	*Mollinedia lanceolata*	3.6	*Spondias mombin*	2.9
		Other Species (15)	12.8	Other Species (32)	27.4	Other Species (24)	43.7	Other Species (49)	64.0
Poles	1	*Cecropia membranacea*	22.4	*Inga sertulifera*	34.6	*Coccoloba williamsii*	15.9	*Virola surinamensis*	7.0
	2	*Tessaria integrifolia*	21.1	*Margaritaria nobilis*	14.2	*Tabernaemontana sananho*	8.4	*Gallesia integrifolia*	5.0
	3	*Inga marginata*	18.3	*Ficus insipida*	6.3	*Virola calophylla*	8.0	*Astrocaryum murumuru*	3.9
	4	*Senegalia polyphylla*	9.9	*Guatteria scytophylla*	5.7	*Pleurothyrium bifidum*	7.1	*Leonia crassa*	3.5
	5	*Salix humboldtiana*	4.2	*Sapium glandulosum*	4.0	*Nectandra purpurea*	7.0	*Pleurothyrium bifidum*	3.2
	6	*Guatteria scytophylla*	3.1	*Cecropia membranacea*	3.8	*Sapium marmieri*	6.1	*Randia armata*	2.9
	7	*Ochroma pyramidale*	2.7	*Inga macrophylla*	2.8	*Guarea macrophylla*	4.6	*Sloanea eichleri*	2.9
	8	*Trema micrantha*	2.6	*Inga marginata*	2.7	*Gallesia integrifolia*	4.4	*Inga marginata*	2.9
	9	*Acalypha mapirensis*	2.2	*Cordia tetrandra*	2.5	*Cordia nodosa*	4.2	*Ficus insipida*	2.9
	10	*Croton lechleri*	2.2	*Croton lechleri*	2.4	*Trichilia maynasiana*	4.1	*Hasseltia floribunda*	2.6
		Other Species (14)	11.2	Other Species (22)	21.0	Other Species (21)	30.0	Other Species (54)	63.1
Trees	1	*Inga marginata*	30.7	*Ficus insipida*	23.9	*Sapium marmieri*	32.8	*Astrocaryum murumuru*	6.6
	2	*Cecropia membranacea*	24.3	*Inga sertulifera*	12.9	*Pourouma cecropiifolia*	9.3	*Virola surinamensis*	6.3
	3	*Trema micrantha*	6.6	*Cecropia membranacea*	11.1	*Erythrina poeppigiana*	8.7	*Guarea macrophylla*	5.0
	4	*Senegalia polyphylla*	6.0	*Inga marginata*	9.8	*Senegalia polyphylla*	6.3	*Spondias mombin*	4.9
	5	*Tessaria integrifolia*	3.9	*Senegalia polyphylla*	6.2	*Guazuma crinita*	5.5	*Brosimum lactescens*	4.7
	6	*Salix humboldtiana*	3.4	*Inga heterophylla*	5.5	*Guazuma ulmifolia*	4.1	*Inga sertulifera*	3.7
	7	*Senna herzogii*	3.2	*Cordia tetrandra*	5.2	*Annona pittieri*	3.2	*Dendropanax arboreus*	3.5
	8	*Inga sertulifera*	3.1	*Ochroma pyramidale*	4.5	*Cordia sp1*	3.2	*Inga marginata*	3.2
	9	*Ochroma pyramidale*	3.0	*Guazuma ulmifolia*	2.6	*Zanthoxylum sp1*	3.0	*Gallesia integrifolia*	2.9
	10	*Margaritaria nobilis*	2.7	*Cecropia engleriana*	2.4	*Coccoloba williamsii*	2.7	*Leonia crassa*	2.5
		Other Species (11)	13.2	Other Species (19)	15.8	Other Species (18)	21.2	Other Species (55)	56.7

†IV = importance index.

the reference forest (Fig. S2).

3.2. Floristic composition

Non-parametric multidimensional scaling and PERMANOVA analyses indicated significant differences in the floristic composition among successional stands and reference forest (*Pseudo-F* = 69, $p < 0.01$) (Fig. 4). PERMANOVA *a posteriori* pair-wise comparisons suggest that floristic composition among the 5, 11 and 23-year-old stands, and the reference forest were significantly different ($p < 0.01$).

The first NMDS axis was directly correlated with species density (^{0}D, rho = 0.76, $p < 0.01$), abundance (rho = 0.50, $p < 0.01$), effective numbers of species (^{1}D: rho = 0.74, $p < 0.01$, and ^{2}D: rho = 0.56, $p < 0.01$), basal area (rho = 0.78, $p < 0.01$), average tree height (rho = 0.80, $p < 0.01$), and average tree DBH (rho = 0.70, $p < 0.01$). The second NMDS axis was significantly but only weakly correlated with species density (^{0}D, rho = 0.40, p < 0.01) and abundance (rho = 0.49, p < 0.01). However, the second NMDS axis was not significantly correlated with effective numbers of species (^{1}D: rho = 0.30, $p > 0.05$, and ^{2}D: rho = 0.31, $p > 0.05$), basal area (rho = 0.20, $p > 0.05$), average tree height (rho = -0.14, $p > 0.05$), and average tree DBH (rho = 0.14, $p > 0.05$). These findings suggest that the NMDS reflects a recovery gradient in composition and species diversity toward mature tropical rainforests (Fig. 4).

The floristic similarity between successional stands and reference forest increased with time since abandonment (Table 4). For mature trees, average Chao-Jaccard similarity values increased from 11.4 % in the 5-year-old stand to 19.3 % in the 23-year-old stand.

Fig. 3. Heat map of indicator values (IndVal) for each successional forest indicator species in the chronosequence and the reference forest by stage of development. The heat map shows the relative abundance of the species in each stand.

For poles, average similarity index values increased from 12.7 % to 22.3 % across the same successional stands. The average Chao-Jaccard similarity index values for saplings increased from 11.9 % to 22.3 %. For mature trees and saplings, floristic similarity among plots of the same successional age were lowest for the reference forest (Table 4a, c). However, for poles, the similarity of species composition among plots of the same successional stands, was lowest for the 23-year-old stand and the reference forest (Table 4b).

3.3. Successional categories and dispersal syndrome

In the reference forest, 6.2 % were pioneer, 35.4 % were early secondary, and 49.2 % were late secondary species. In the chronosequence, the proportion of late secondary species was lower but increased from 18.5 % in the 5-year-old stand to 38.9 % in the 23-year-old stand. Conversely, the proportion of pioneer species decreased through the chronosequence, from 44.4 % in the 5-year-old stand to 7.4 % after 23 years of abandonment (Fig. 5a).

Considering all species, we found zoochory in 76 % of the species, followed by anemochory (21 %), and autochory (3 %). The proportion of zoochorous species throughout the chronosequence increased from 66.7 % after 5 years to 81.5 % after 23 years of abandonment (Fig. 5b). Conversely, the proportion of anemochorous species in the chronosequence decreased from 25.9 % after 5 years to 16.7 % after 23 years of abandonment (Fig. 5b).
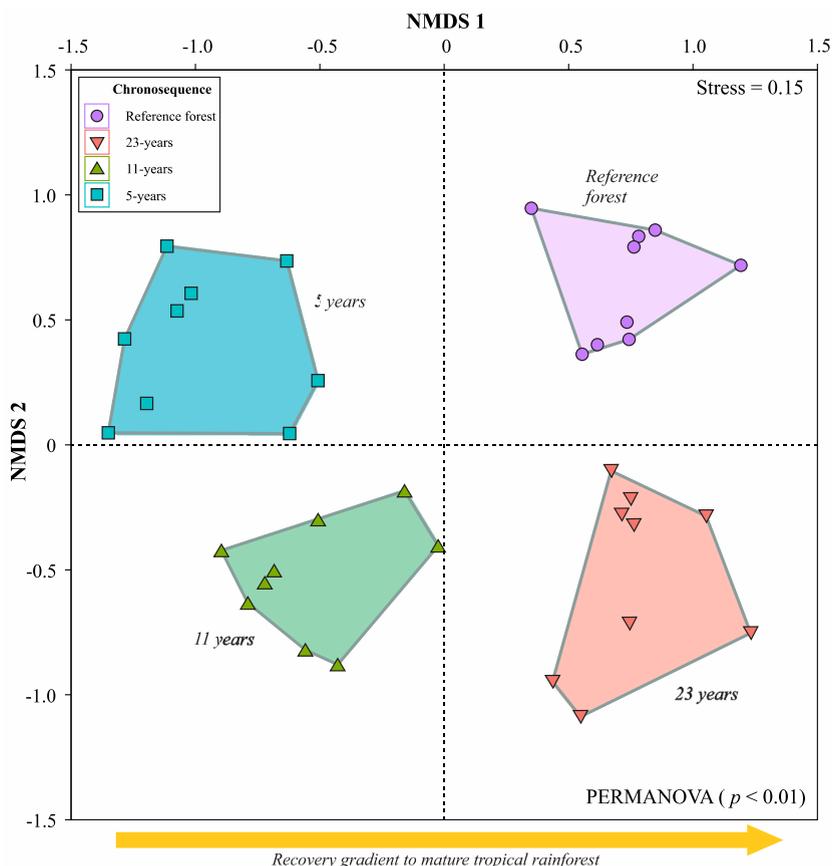
Fig. 4. Based on abundance data using the Chao-Jaccard distance matrix, the floristic composition is summarized in two dimensions derived from the non-metric multi-dimensional scaling (NMDS). Each point symbolizes a single sub-plot of stands in the chronosequence. Colors indicate the three stands with different periods of time after mining and the reference ecosystem.

Table 4
Average pairwise Chao-Jaccard Similarity Index among stands in the chronosequence based on square root transformed abundance of (a) mature trees, (b) poles and (c) saplings. Bold numbers represent the similarity between plots of the same time since abandonment.

	Time since abandonment				Reference forest
		5-years	11-years	23-years	
(a) Mature Trees	5-years	**72.1**			
	11-years	23.4	**66.7**		
	23-years	3.3	9.4	**69.1**	
	Reference forest	11.4	18.7	19.3	**56.4**
(b) Poles	5-years	**78.4**			
	11-years	32.8	**74.8**		
	23-years	4.3	7.7	**77.6**	
	Reference forest	12.7	17.6	22.3	**72.6**
(c) Saplings	5-years	**66.2**			
	11-years	37.3	**73.0**		
	23-years	10.6	24.0	**79.3**	
	Reference forest	11.9	14.9	22.3	**67.1**

4. Discussion

4.1. Changes in diversity, floristics and forest structure

The increase in diversity and species density in the chronosequence in Madre de Dios forests suggests a fast recovery after abandonment of gold mining [48,49] compared with recent studies in degraded areas by gold mining in Madre de Dios [21,22]. Species
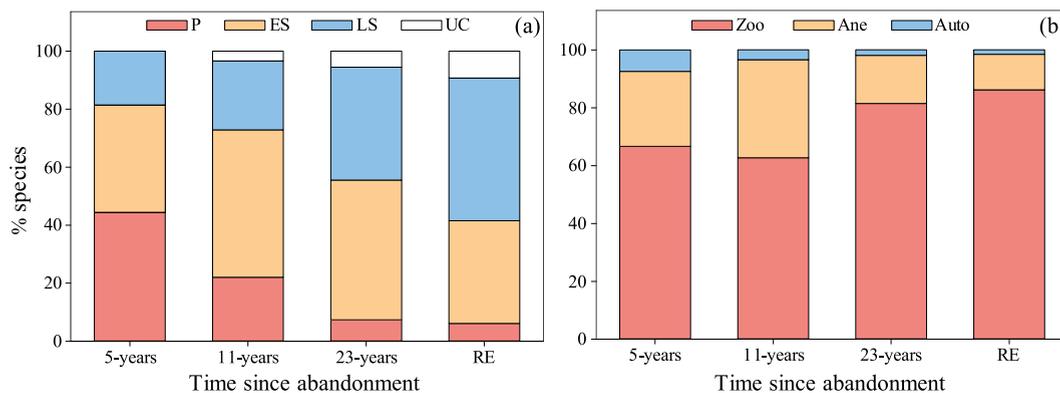
Fig. 5. Percentual distribution of species of three stands with different periods of time after mining and reference forest (RE) by (a) successional category (P, pioneer species; ES, early secondary species; LS, late secondary species; UC, unclassified) and (b) dispersal syndrome (Ane: anemochory; Zoo: zoochory; Auto: autochory).

density of natural regeneration was between 2.6 and 4.1 times higher in the present study than those reported by Alarcón-Aguirre et al. [21] and Garate-Quispe et al. [22]. These differences are probably due to the small spatial scale of the mined areas in the study area, which did not affect the landscape connectivity and proximity of the reference old-growth forest. Because in the study area of Alarcón-Aguirre et al. [21] and Garate-Quispe et al. [22] the mining activities are widespread and generate a high level of landscape fragmentation, thus limiting seed dispersal and woody plant establishment.

Species density and tree diversity increased significantly during succession as early as secondary successional species became established. Still, a decline in pioneer species in the later successional stage is observed due to competition that leads to dominance of late secondary species [3,50]. Species density and diversity were higher in smaller DBH classes (like saplings) than in the tree category. These results are congruent with other chronosequence studies of secondary succession, including those by Alarcón-Aguirre et al. [21] in succession sites after gold-mining in southeast Peruvian Amazon, and by Peña-Claros [51] in a 40-year-old stand after crop abandonment in Bolivian Amazon, by Marín et al. [25] in a 14-year-old stand after crop abandonment in Nicaragua, by van Breugel et al. [26] in succession sites in lowland tropical forest of Mexico. The high species diversity of saplings in successional forests is a good indicator of biodiversity recovery and sustainability of recovery after gold-mining [21]. This may suggest this category is represented by species that overcame the filters or barriers of dispersion and establishment [52].

A different pattern was observed in the reference forest, where species density and diversity of saplings were lower than that of trees. Similar results were found by Comita et al. [53] in primary tropical forests and by Dent et al. [54] in a secondary forest chronosequence of Panama. This difference in diversity patterns of saplings and trees among successional forest and reference forest suggests that recruitment limitations are lower in successional forests than in the reference forest where resources (such as space and light) are scarce. Furthermore, in primary forest succession, species of saplings represent a subset of those species that eventually reach the canopy [48,53].

Another key finding was that species density recovered following mining abandonment to around 77 % after 23 years. The same pattern of biodiversity recovery was found in Neotropical secondary forests, which highlights the resilience of biodiversity to anthropic impacts [55,56]. Similar results were found by Rodrigues et al. [29] in an area degraded by mining in Brazilian Amazon and by Peña-Claros [51] in secondary succession in the Bolivian Amazon. On the other hand, *C. membranacea* is regenerating in the 5-year-old stand. This indicates that light enters the understory because the canopy is still open. In other areas of the Amazon, a 5-year-old secondary forest already has a closed canopy and almost no *Cecropia* saplings. Even though mining causes deforestation and severely impacts soil quality, there is a faster recovery of floristic and structural attributes than species composition. Mainly due to pioneer species in 5-year-old stands, a similar pattern is experiencing natural disturbances.

In contrast to previously described patterns of floristic composition and forest structure, change in stem density was not related to time since abandonment of gold mining [11,51]. Our results suggest that floristic composition and species dominance were essential factors that influenced tree stem density in the initial and intermediate successional stages [23]. High densities of a few pioneer species in the initial successional stages may be related to their rapid growth and recruitment of these light-demanding species [57,58]. Other forest succession studies in abandoned mining fields, including Rodrigues et al. [29], Brady and Noske [59], Rocha-Nicoleite et al. [5], and Alarcón-Aguirre et al. [21], found similar results. On the other hand, low stem densities in the advanced successional stage suggest a high density-dependent mortality rate during the initial successional stage, which then provides recruitment opportunities for early and late secondary species [26].

Forest stand structure recovered rapidly through the chronosequence, because canopy height and basal area in the 23-year-old stand were about 72 % and 40 % of the reference forest, respectively [60]. These suggest that favorable conditions are being created as succession progresses for the establishment and growth of later successional tree species [26,61]. In tropical Amazon secondary forests, structural characteristics of vegetation recovered faster than species composition [62,63]. Similar results were found by Aráujo et al. [27] in an area degraded by kaolin mining, Miranda-Neto et al. [28] after bauxite mining, Rocha-Nicoleite et al. [5] and other non-mining chronosequence studies [30,64]. In tropical forest recovery of species diversity occurs at an intermediate to

slow pace (4–6 decades) in comparison to very fast recovery of forest structure (2.5–5 decades), and slow for biomass and species composition (>12 decades) [56].

Few species were dominant in the stands studied, and their dominance decreased during succession, particularly in the smaller size classes. Similar results were found by van Breugel et al. [26] in secondary succession of abandoned pastures in Mexico and Alarcón-Aguirre et al. [21] in lands degraded by gold mining in the Peruvian Amazon. As in other studies, in this one species dominance differed between the chronosequence stands and the reference forest [26]; dominance was higher in young stands, particularly in the canopy layer where pioneer trees dominated [51]. These dominance patterns are congruent with other chronosequence studies in secondary succession, including those by Marín et al. [25] and Guariguata and Ostertag [24].

The short-lived *C. membranacea* and *O. pyramidale* are common on lands degraded by gold mining in Madre de Dios, where seed-rain is the main source of species recruitment because the soil is highly disturbed and without a seed bank [65]. Due to its fast growth, *C. membranacea* generates a stratified canopy [30] that allows the establishment of early successional species, driving rapid turnover in floristics composition and quicker recovery after disturbance [23,66]. Other species such as *T. integrifolia* provide a more suitable environment for germinating tree seedlings [11]. Therefore, the high density of pioneer species in initial successional stages is important because these generate favorable conditions for establishment of early and late secondary species and reestablishment diversity [29,66], and should not be disregarded in recovery practices of abandoned fields after mining [22]. In intermediate successional stands, sapling and pole layers were dominated by early and late secondary species. *F. insipida* (ES), *I. sertulifera* (ES) and *C. membranacea* (P) dominated the overstory tree layer, and they are more abundant in young than in old forests [64,67]. Nevertheless, typical late secondary species dominated the reference forest. Thus, the ten most dominant species in the reference forest represented less than 43 % of the importance index, which is a lower value than those reported by van Breugel et al. [26].

Urticaceae and Asteraceae were important for the initial successional stage because they are widespread and abundant in the seed banks of young tropical forests [68]. Conversely, Malvaceae increased its importance with time since abandonment, which means it is a typical part of the old-growth forests in the Amazon [54]. Fabaceae had the highest species density, dominance, and abundance in the chronosequence stands and reference forest [25,30]. Species of Fabaceae may be especially suitable for restoration because they can increase the nitrogen in degraded soil [5,24,69]. Fabaceae species would thus facilitate the establishment and growth of other species [69].

4.2. Floristic composition

Floristic similarity in stands for a given time since abandonment was higher in the successional forests than in the reference forest but increased across the chronosequence [64]. For trees, the highest similarity was found when comparing the floristic composition between the 5- and 11-year-old stands due to the dominance of pioneer species [70]. Floristic similarity showed a slow recovery through the chronosequence compared with forest structure parameters [55,56]; these findings are consistent with other recent studies of natural regeneration in degraded land by gold-mining in Madre de Dios [21,22]. Floristic similarity among the successional stands and reference forest increased as one moves through the chronosequence. Similar results were reported by Suganuma and Durigan [52] in post-agriculture/pasture restoration land in the Brazilian Atlantic Forest [64].

Moreover, based on ordination pattern and similarity analysis, the increase in floristic similarity through the chronosequence exhibits a convergent trajectory toward the reference forest [2,59]. Some authors suggest this is due to a slow recovery in plant communities early in the chronosequence [71]. However, it could also be due to the dispersion and establishment of additional species. This accords with the finding that the sapling, pole, and mature tree categories in the 23-year-old stand and the reference forest were dominated by different species. That said, our chronosequence is too small to draw conclusions about the final pattern of convergence or divergence. However, Prach and Walker [4] also studied abandoned mining sites and found that divergent trajectories in species composition are more common.

4.3. Successional categories and dispersal syndrome

Proximity of the chronosequence stands to the reference forest, which could promote species dispersal in the initial and intermediate successional stages since most species are zoochorous. Our results are like those found by Alarcón-Aguirre et al. [21] in degraded areas by gold-mining in Madre de Dios, and other similar studies such as Aráujo et al. [27] in areas degraded by kaolin mining, Miranda-Neto et al. [28] at a bauxite mine, and Rocha-Nicoleite et al. [5] after severe degradation by coal mining in Brazil. However, the proportion of zoochorous species in these studies was higher than in cases of non-mining secondary succession in the Brazilian Amazon [66,72]. Many studies in tropical secondary forest succession show a significant negative relationship between distance from forest fragment edge and seedling establishment [61,73] and species richness in the seed rain [29,61]. As found in the present study, the dominant dispersal syndrome of species can vary during succession. The proportion of zoochorous species is usually higher at the later stage of succession and in the reference forest [5,60,73], and increased through the chronosequence. Conversely, the proportion of anemochorous species is usually higher in initial successional stage and decreased through the chronosequence [5,27]. This pattern occurred because wind-dispersed species have a better chance than animal-dispersed species to reach abandoned mining areas far from forests [74]. Wind-dispersed species are also the most frequent means of dispersal into abandoned pastures in Puerto Rico [61]. In the initial succession stages, colonizing plants have tiny seeds adapted for wind dispersal, while in later succession, heavier seeds arrive more slowly [75].

The high proportion of pioneer species and the low proportion of late secondary species in the initial succession stages can be explained by dispersal, plasticity, and acclimation capacity of those species. According to Strauss-Debenedetti and Bazzaz [76],

pioneer species have high photosynthetic plasticity and high acclimation capacity under high irradiance conditions, being more efficient using resources (such as water and nutrients) and growing at higher rates. In contrast, late secondary species have a lower acclimation capacity under high irradiance conditions [76,77]. Moreover, we found an increase of shade-tolerant species through the chronosequence, which suggests changes in dominance from pioneers to early and late secondary species. Similar patterns were also reported for secondary succession in Bolivia, Brazil, and Mexico [26,29,51].

4.4. Limitations and suggestions for future research

This study has certain limitations. Our conclusions could be limited by the small sample size of the forest regenerated after mining activities (three forest sites) because the study focused solely on degraded areas in a native community of Madre de Dios, which affects generalizability of the results. Therefore, more studies are needed at a regional level to enhance the study's findings and focus on primary ecological indicators of natural regeneration [78]. Second, the current study used chronosequence approach (cross-sectional data) and future studies need to be longitudinal (i.e. permanent plots) to monitor the forest and confirm the vegetation's recovery over time. Despite these limitations, our results are consistent with other studies in secondary successions [26,29,66,72,79], and provides new insights for a deeper understanding of natural regeneration in areas degraded by gold mining in the Peruvian Amazon. In future studies we will analyze differences in structure, above ground biomass, floristic attributes (e.g., diversity), and floristic composition among different types of mining operations, edaphic conditions, and stands age. Likewise, functional species traits [79] and influence of distance to the forest edge on recovery of degraded areas by gold-mining [62] will be considered. Also, pioneer tree species should be carefully selected to create an optimum understory condition to promotes active restoration [80]. Ecological restoration is a highly viable approach to address climate change and preserve ecosystems [81]. However, in restoration activities have frequently relied on standard plantation techniques applied over large areas, without regard for the small-scale spatial variability of favorable microsites [82]. In future research succession studies after mining, the first step should be a review of previous studies to avoid duplication and understand the main advances and gaps remaining [78] and we recommend the use of permanent plot as a supplement of chronosequence studies to validate the results throughout time [62,83].

5. Conclusions

Amazon tropical forests are usually highly resilient to severe disturbances (i.e., logging, agriculture, and mining). In our study area, where mining does not destroy vast areas of old growth forest, it creates a gap pattern that allows the establishment of pioneer tree species as we have demonstrated. The floristic and structural attributes of the forest throughout the chronosequence showed a fast recovery. The forest structure recovers faster than the floristic composition. Natural assisted regeneration could be the most cost-effective option for gold mining in the study area.

The high proportion of zoochorous tree species in the 5-year-old stand and the increase of these species throughout the chronosequence highlight the importance of animal seed dispersal in abandoned gold-mining lands. Therefore, we recommend using the most abundant native species found in the present study in the forest restoration of degraded lands.

Data availability statement

Data will be made available on request.

CRediT authorship contribution statement

Jorge Garate-Quispe: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ramiro Canahuire-Robles:** Methodology, Investigation, Data curation, Conceptualization. **Gabriel Alarcón-Aguirre:** Writing – review & editing, Formal analysis. **Hugo Dueñas-Linares:** Writing – review & editing, Validation, Conceptualization. **Francisco Roman-Dañobeytia:** Writing – review & editing, Visualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e29908.

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