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Resilience of Aboveground Biomass of Secondary Forests Following the Abandonment of Gold Mining Activity in the Southeastern Peruvian Amazon

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Abstract: Amazon rainforests are critical for providing a wide range of ecosystem services. In the Southeastern Peruvian Amazon; however, goldmining activities are causing severe soil degradation and forest loss. We analyzed aboveground biomass (AGB), forest structure, and species diversity recovery during secondary succession in 179 forest plots. Our study provides the first field-based quantification of AGB recovery following the abandonment by two types of goldmining (heavy machinery and suction pumping) in Madre de Dios (Peru). We found that successional secondary forests in areas subjected to suction pumping were more resilient than those in areas subjected to heavy machinery. After 20 years, mean AGB in suction pumping mining areas had reached 56% of reference forest AGB, while in areas of heavy machinery mining it was only 18%. Mining type, stand age, and distance from the forest edge had a significant effect on AGB. The influence of the distance from the forest edge on AGB varies according to mining type because the effects of species diversity on AGB are mediated by the distance from the forest edge. Our results clearly showed the dynamics of AGB recovery across a secondary succession after goldmining, and the contrasting responses of AGB between the two mining types. Our study disentangles the importance of key factors in forest recovery after mining and improves understanding of the resilience of biomass accumulation in these highly degraded ecosystems.

Keywords: chronosequence; ecological succession; forest recovery; forest structure; Madre de Dios; natural regeneration; recovery of impacted areas; species composition; species diversity

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1. Introduction

Tropical forests are a crucial component of the Earth system [1], because they harbor great biodiversity (63% of tree species globally) [1] and provide carbon storage, which is relevant to the regulation of global climate change [2,3]. These forests are being transformed rapidly as a result of human activities [4]. Such deforestation and forest degradation generate between 10 and 15% of global greenhouse gas emissions [5]. Therefore, its loss would have a significant impact on climate change [6]. In addition, the Amazon rainforests are very important for providing hydrological services and harboring a high species diversity [7].

The mining industry is essential for the development of the world economy and human societies [8,9]. Although mining activities occur on a small fraction of the Earth's land surface (less than 1%) [8], they can generate severe environmental impacts [10,11] and have potentially adverse effects on the health of the local population [12], as well as representing one of the most serious threats to tropical ecosystems. [13,14].

More than half of the global forests are disturbed and knowing the rate of forest recovery is important for estimating the ecosystem services that these forests can provide [15]. Despite the importance of tropical forests and their high levels of degradation, they remain poorly monitored [7]. The Amazon forests of Madre de Dios are being affected by rapid economic and population growth, and among all human activities, gold mining generates the most severe impacts [16]. Goldmining causes severe environmental degradation through deforestation, mercury pollution, and soil degradation and eliminates the capacity of ecosystems to accumulate biomass [16]. However, areas degraded by mining are not usually evaluated because they occupy relatively small land areas [17].

Land use changes in tropical forests, however, are occurring at a faster rate than in other regions of the planet, and this imbalance between deforestation and forest restoration has serious effects on the global carbon cycle [18]. Agriculture and goldmining are the primary drivers of deforestation in the southern Peruvian Amazon [19], although mining activity causes the most severe impacts [20,21]. The resilience of these ecosystems after abandonment by mining activities remains to be studied in detail [21]. Forest biomass is key in the carbon cycle process and is being studied in the context of international climate change mitigation initiatives. [22]. Information on how these areas are recovering after abandonment will allow the generation of more sustainable management models and identify potential sites for future carbon sequestration projects [18]. In this context, aboveground biomass (AGB) is a key indicator to determine the dynamics of carbon recovery in degraded ecosystems [15]. Therefore, biomass estimation is important in quantifying the carbon sink flux, measuring international carbon stocks, and mitigating the increasing CO_2 pollution [23].

Recent studies in the Amazon have reported the ecological mechanisms of human activity influence on the recovery of species diversity, species composition, and AGB [24–27]. Many studies have shown that the stand forest age [28,29], species number [30], species diversity [31], species composition [32], and forest height [33] are positively correlated with AGB levels in secondary forests. In addition, a recent study showed that forest structure (e.g., forest height) conditions the effects of species richness on AGB accumulation [24]. Other factors that may limit the AGB recovery are the degree of land use intensity and soil degradation [34]. Studies of AGB recovery after goldmining in the Amazon are particularly rare. Nevertheless, Kalamandeen et al. [21], in a recent study in the Amazon region of Guyana, found that areas severely degraded by gold mining have a slow biomass recovery compared to other secondary forests (e.g., from agriculture or pasture).

AGB accumulation and changes in species diversity and species composition in primary forests and secondary forests have been monitored in several studies [35,36]. These have shown that secondary forests are an important carbon sink, and in some cases, they can be higher than primary forests [7]. This highlights the importance of secondary forests in mitigating climate change and promoting biodiversity recovery [37]. For this purpose, the chronosequence approach has been one of the most widely used [38]. However, there are few studies that analyze the recovery of biomass in secondary succession after abandonment by mining activities [39], compared to studies in areas degraded by other activities such as agriculture or livestock [21].

In the Southeastern Peruvian Amazon (Madre de Dios), studies on biomass estimates in natural regeneration after abandonment by mining activities are scarce. Most studies have focused on assessing the species diversity, floristic attributes, species composition [20,40,41], reforestation/rehabilitation experiments of these degraded ecosystems [42–46], and monitoring forest loss due to goldmining [19,26]. These studies showed that the degree of resilience of tree communities after abandonment by mining activities depends on the level of landscape fragmentation [41], stand age [20], and distance from the forest edge [41]. Meanwhile, the experiments in these areas demonstrated the rapid acclimatization of native tree species [44,46,47] and cover plants [43] to these severely degraded environments.

This study addresses the recovery of aboveground biomass (AGB) from secondary forests according to two types of mining (heavy machinery and suction pumping) following the abandonment of gold mining activity in the Southeastern Peruvian Amazon. We posed the following research questions: (1) What are the AGB, forest structure, species diversity, and floristic composition of a secondary succession across a chronosequence after 23 years of abandonment? (2) What is the influence of mining type, stand age, and the distance from the forest edge on AGB, forest structure, and tree species diversity of the regenerating community? (3) How do our results in secondary forests after mining compare with reference forests? (4) How is the AGB accumulation affected by stand age, distance from the forest edge, and species diversity according to mining type?

2. Materials and Methods

2.1. Study Area

The study was conducted at 11 mining sites in the Madre de Dios region, Southeastern Peruvian Amazon (Figure 1). The study area is classified as a tropical Amazon forest [46] with an altitude ranging from 220–450 m above sea level. The study area is characterized by warm, humid, and seasonal weather conditions. The annual average rainfall ranges between 1500 mm and 2860 mm [48]. The average annual temperature is around 25 °C, ranging from 16 °C to 39 °C. During the dry season, from June to September, precipitation is lower than 100 mm per month [39,41] (Figure S1).

The forest types that covered the study area were low-terrace forest and low-hill forest [49]. The canopy reaches a height of up to 40 m, with some emergent trees that can reach up to 60 m. Low-terrace forests are located in the alluvial plain of the lowland rainforest, occupying both recent low terraces (floodable) and ancient terraces (non-floodable). Recent low terraces are usually dominated by *Ficus insipida*, *Calycophyllum spruceanum*, *Euterpe precatoria*, *Garcinia macrophylla*, *Astrocaryum murumuru,* and *Sloanea guianensis*. While ancient terraces are usually dominated by *Bertholletia excelsa* (that reach heights up to 60 m and DBH up to more than 2 m), *Myroxylum balsamun*, *Clarisia racemosa*, *Spondias mombin*, *Hevea guianensis,* and *Iriartea deltoidea*. Low-hill forests develop in lands originated by very ancient fluvial deposits, and they are dominated by *Pseudolmedia laevis*, *Astrocaryum murumuru*, *Oenocarpus bataua*, *Brosimum alicastrum,* and *Cedrelinga cateniformis* [49]. In tropical Amazon forest the proportion of zoochorous species is usually higher in old-growth forests and at the later stage of secondary forests [11,50], and the proportion of anemochorous species is usually higher in the initial successional stage [51].The weathering and erosion of hard rock ores in the Andes produced fine grains of gold. These were carried down the rivers to the lowlands of Madre de Dios, forming placer deposits. These fine gold particles settle in river meanders and form near-surface deposits in floodplains due to changes in river geomorphology and seasonal flooding [52].

At selected sites, two types of mining (heavy machinery and suction pumping) are applied for gold extraction. In suction pumping mining, miners used the open-pit method to extract gold. Such operations require cutting all aboveground vegetation and removing the soil. When dredging, gold-containing soils are pumped from deep pits (up to 10 m) to a sluice box to collect the gold particles [41] (Figure 1C). In highly mechanized mining the gold particles are extracted by excavation using heavy machinery such as front loaders, excavators, and dump trucks for sediment transportation to a sluice box [53,54] (Figure 1C). For this reason, heavy machinery mining causes more deforestation and environmental damage than suction pumping [52]. After mining activities, these areas are abandoned without any strategy for soil or vegetation recovery. The study was conducted in areas degraded and abandoned by goldmining activity, where the vegetation had regenerated naturally.

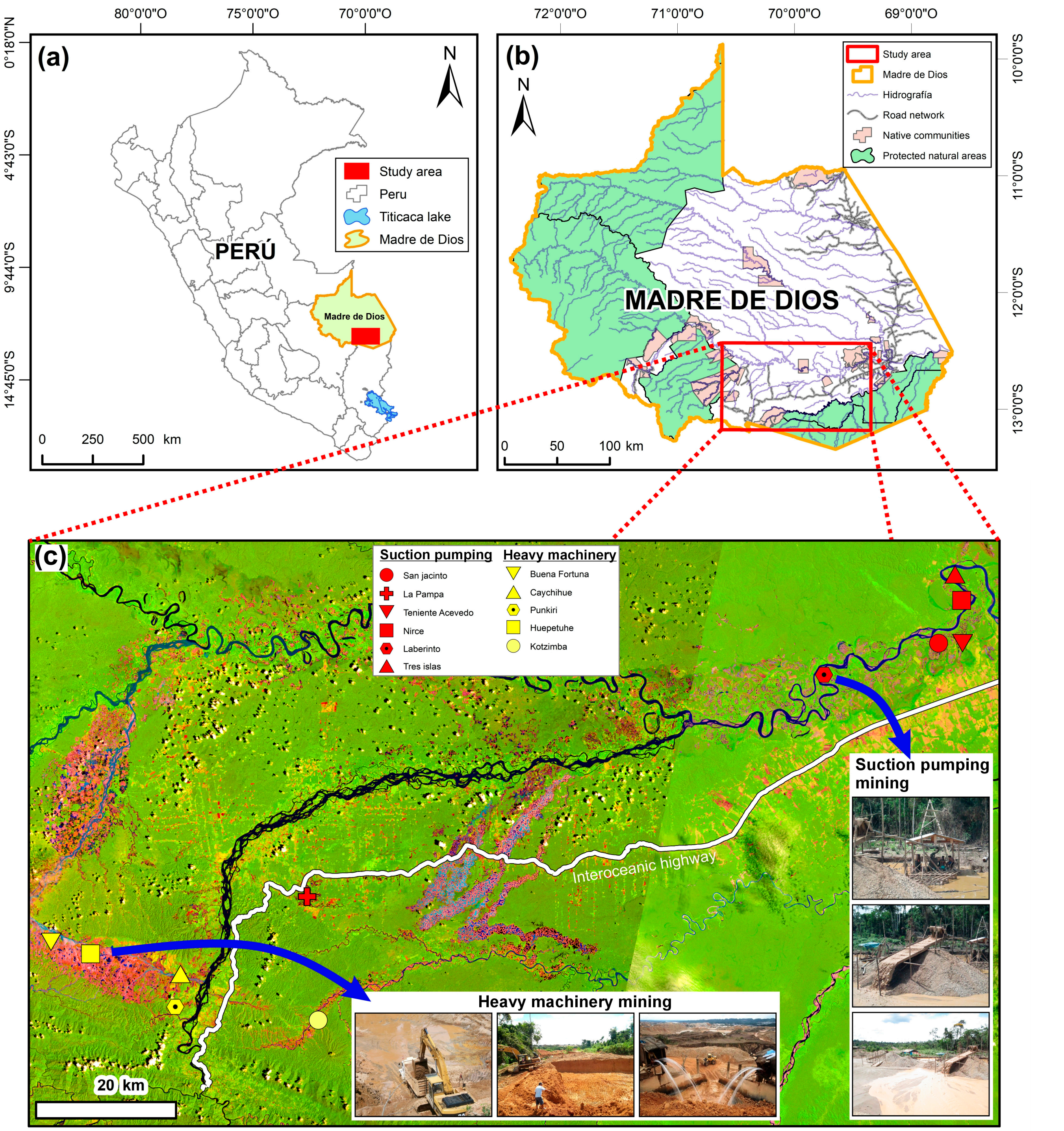

Figure 1. Map of the study area in Peru (**a**) and in Madre de Dios (**b**), Southeastern Peruvian Amazon. (**c**) Landsat-8 images (July 2023) over the study. It shows the location of field sites in the study, and representative photos of the type of mining.

2.2. Study Design and Vegetation Sampling

We compiled data from 11 chronosequence studies (sites) about natural regeneration post goldmine abandonment, including 179 plots, containing 4699 tree stems. For 4 out of the 11 sites, reference forest plots were included (Table 1). We included 17 reference forest plots near the areas where natural regeneration was evaluated, which contained 1139 tree stems. The reference forest has never been affected by goldmining activities for at least 40 years.

Table 1. Number of forest plots sampled in secondary forest after mining abandonment and in the reference forest in the Peruvian Amazon.

N	Site	Mining Type	Number of Plots in Secondary Forest	Distance from the Forest Edge (m)			Stand Age (Years)			Number of Plots in Reference Forest
				Mean ± SD	Min	Max	Mean	Min	Max	
1	Buena Fortuna	Heavy machinery	6	733	550	900	18	17	20	
2	Kotzimba		3	333	230	500	8	4	9	
3	Caychihue		19	607	340	943	10	4	16	
4	Huepetuhe		8	675	600	900	24	24	16	4
5	Punkiri		16	91	25	280	10	7	15	8
6	Laberinto	Suction pumping	14	64	22	152	9	2	19	
7	Nirce		27	272	95	517	10	4	22	
8	Teniente Acevedo		50	617	180	940	7	2	14	
9	Tres islas		12	35	15	70	15	5	23	3
10	La Pampa		6	82	10	176	8	6	12	2
11	San Jacinto		18	175	29	520	8	2	23	
		Total	179	-	-	-				17

Plot size varied from 0.01 to 0.25 ha, with a length varying from 10 to 60 m and width ranging from 10 to 60 m. The size of the plot area varies according to that used in the studies compiled. In addition, the use of small plots is due to the reduced size of areas with natural regeneration after abandonment by mining (varying from 0.05 to 1 ha). In each sample plot, the height and diameter at breast height (DBH; 1.3 m aboveground) of all woody trees with stems $\geq$ 5 cm were measured [55,56]. We excluded trees with DBH < 5 cm because they represent a small proportion of AGB in forests [56].Stand age and the distance from the forest edge for each plot were determined by using multi-temporal Landsat (1975–2010), RapidEye, and Planet imagery (2010–2023). In the case of stand age, this was complemented by interviewing landowners. In this study, the distance from the forest edge was considered as a proxy for fragmentation.

All trees were identified and their AGB estimates made using allometric equations. Species were classified according to the APG IV [57]. Scientific names were revised and corrected using the TNRS application (https://tnrs.biendata.org, accessed on 15 January 2024).

2.3. Aboveground Biomass (AGB)

Aboveground biomass (AGB) was calculated, for all trees present in the plots, using the generic pan-tropical allometric biomass equation developed by Chave et al. [58] (Equation (1)):

$$AGB = 0.0673 \times \left(\rho \times DBH^2 \times H\right) \tag{1}$$

where AGB is aboveground biomass in kg, H is the tree height in m, D is the diameter at breast height in cm, and ρ is the wood density in gr cm^{-3}. The wood density of trees was obtained from the global wood density database [59].

Individual tree biomass values within the plot were summed and converted to AGB stock (Mg ha^{-1}) [60]. In order to assess how fast the AGB of the secondary forest is recovering towards the values of the reference forest, we calculated the relative AGB recovery as the AGB of the secondary forest plot compared to the mean AGB of the reference forest plots in the study area [18].

2.4. Stand Structure and Alpha and Beta-Diversity Calculations

Forest structure was analyzed by structural indices [58]; we calculated in each plot: (a) the mean of the DBH of all woody species, and (2) the mean of the height of all woody species. In addition, to examine the horizontal structure of the communities [61] we calculated the importance value index (IVI) of each species according to five recovery age classes of natural regeneration and reference forest. The IVI was computed using the method of Curtis and Macintosh [62], using R package BiodiversityR [63]. IVI was computed as follows (Equation (2)):

$$\text{IVI}(\%) = \frac{\text{Abun}(\%) + \text{Dom}(\%) + \text{Frec}(\%)}{3} \tag{2}$$

where IVI (%) is the importance value index, Abun (%) is the relative abundance, Dom (%) is the relative dominance, and Frec (%) is the relative frequency.

We used effective numbers of species (Hill numbers) to quantify the species diversity of each plot. Hill numbers are a mathematically unified family of diversity indices that incorporate relative abundance and species richness [64]. The calculations were performed using the R package hillR [65] for the three components of species diversity represented by the Hill series (^{0}D, species richness weighting all species equally; ^{1}D, exponential of Shannon's entropy index weighting typical species; ^{2}D, inverse of Simpson's concentration index weighting dominant species).

For taxonomic β-diversity, to quantify differences in tree community composition among plots, we used the abundance-based Chao–Jaccard dissimilarity index. Chao–Jaccard index was calculated using the R package CommEcol [66].

2.5. Data Analysis

We used both structural equation models (SEM) and generalized linear models (GLM) to disentangle the relative effects of stand age, distance from the forest edge, and species diversity on AGB accumulation according to mining type.

GLMs were used to test for an effect of mining type, stand age, and distance from the forest edge on AGB, species diversity (Hill numbers), and forest structure. For AGB data the Tweedie distributed responses were assumed because data were overdispersed [67]. Whereas Poisson distribution function was used for species diversity (^{0}D, ^{1}D, and ^{2}D) and forest structure (mean DBH and mean height).

To assess the direct and indirect effects of stand age, distance from forest edge, and species diversity (Hill ^{0}D) on AGB, three structural equation models (SEMs) were carried out for the following: (1) each type of mining and (2) all data without differentiating by type of mining. Structural equation modeling was conducted using the "lavaan" package in R [68,69]. To determine path coefficients we used the maximum likelihood method because it is robust to multivariate non-normality [70].

We used a one-way ANOVA (Bonferroni's post hoc tests) or Kruskal–Wallis (Dunn post hoc test) test to detect significant differences ($p < 0.05$) in AGB, species diversity, and stand structure among five recovery age classes (binned into five, five-year age classes) of natural regeneration and reference forests. To check whether the data conforms to normality of residuals and homogeneity of variance (homoscedasticity) assumptions to perform ANOVA, we utilized the Shapiro–Wilk test and Levene's test, respectively. If the normal distribution assumption or homoscedasticity was not satisfied, we used the Kruskal–Wallis test instead of ANOVA. When the difference among groups was significant, we used Bonferroni's post hoc tests in ANOVA and the post hoc Dunn's test in the Kruskall–Wallis test.

We used non-linear regression (Gompertz sigmoidal function) to model and compare the changes in AGB and AGB throughout the chronosequence. SigmaPlot 15 was used for curve fitting Gompertz sigmoidal function. Regression parameter estimates and the respective 95% confidence interval values are presented in scatterplots.

Non-metric multi-dimensional scaling (nMDS) plots were used to visualize the tree community composition at natural regeneration stands and reference forests across stand age, sites, and by type of mining. The NMDS was performed in Primer-E 7 using a Type II Kruskal fit scheme with 9999 restarts and based on a similarity matrix of Chao–Jaccard indices. We considered a stress cut-of 0.2, because nMDS plots with stress > 0.2 are unreliable [71].

We used a permutational multivariate analysis of variance (PERMANOVA) to test for differences in species composition between types of mining and across five recovery age classes of natural regeneration. We conducted PERMANOVA analysis using Primer-E 7, where mining type was treated as a fixed effect and stand age and distance from the forest edge were used as covariates. In addition, we used PERMANOVAs to test for interacting effects of mining type, stand age, and distance from the forest edge on species composition after goldmining abandonment.

All statistical analyses were performed using the R statistical software version 4.3.2 [69], SigmaPlot version 15, InfoStat 2020p, and Primer 7 Permanova+.

3. Results

3.1. Effects of Mining Type, Stand Age, and Distance from the Forest on AGB

We found that mining type had a significant effect on AGB (GLM, $p < 0.05$) and species diversity (^{0}D, ^{1}D, and ^{2}D; GLM, $p < 0.001$), but no significant effect was found for forest structure (Table 2), mean DBH (GLM, $p > 0.05$) and mean height (GLM, $p > 0.05$). However, results of the GLM showed that stand age and distance from the forest edge had a significant effect on AGB (GLM, $p < 0.001$; Table 2a), species diversity (GLM, $p < 0.001$; Table 2b–d), mean DBH (GLM, $p < 0.001$; Table 2e), and mean height (GLM, $p < 0.001$; Table 2f). AGB, species diversity, mean DBH, and mean height were positively correlated with stand age and negatively with the distance from the forest edge. Mining type, stand age, and distance from the forest edge explained 73.8% of the variation in AGB (Table 2a).

Table 2. Results of the generalized linear models (GLM) indicating the effects of mining type, stand age and distance from the forest edge on above-ground biomass (AGB), effective number of species (^{0}D, ^{1}D, and ^{2}D), and forest structure (mean DBH and mean height of woody species).

(a) AGB					**(d) Hill ^{2}D**				
Source of variation	**Estimate**	**Std. Error**	***p***	**D^2**	**Source of variation**	**Estimate**	**Std. Error**	***p***	**D^2**
Intercept (heavy machinery)	2.0086	0.1986	<0.001	73.87	Intercept (heavy machinery)	2.0650	0.1040	<0.001	71.57
Mining type (Suction pumping)	0.2972	0.1291	0.023		Mining type (Suction pumping)	−0.5382	0.0731	<0.001	
Age	0.1592	0.0100	<0.001		Age	0.0441	0.0056	<0.001	
Distance from forest edge	−0.0021	0.0002	<0.001		Distance from forest edge	−0.0020	0.0001	<0.001	
(b) Hill ^{0}D					**(e) Mean DBH**				
Source of variation	**Estimate**	**Std. Error**	***p***	**D^2**	**Source of variation**	**Estimate**	**Std. Error**	***p***	**D^2**
Intercept (heavy machinery)	2.3214	0.0848	<0.001	68.52	Intercept (heavy machinery)	2.2480	0.0823	<0.001	57.38
Mining type (Suction pumping)	−0.2468	0.0598	<0.001		Mining type (Suction pumping)	0.0820	0.0540	0.129	
Age	0.0550	0.0043	<0.001		Age	0.0265	0.0039	<0.001	
Distance from forest edge	−0.0024	0.0001	<0.001		Distance from forest edge	−0.0005	0.0001	<0.001	
(c) Hill ^{1}D					**(f) Mean height**				
Source of variation	**Estimate**	**Std. Error**	***p***	**D^2**	**Source of variation**	**Estimate**	**Std. Error**	***p***	**D^2**
Intercept (heavy machinery)	2.0786	0.0970	<0.001	71.65	Intercept (heavy machinery)	2.0645	0.0977	<0.001	58.03
Mining type (Suction pumping)	−0.3930	0.0680	<0.001		Mining type (Suction pumping)	−0.0531	0.0647	0.412	
Age	0.0537	0.0050	<0.001		Age	0.0187	0.0048	<0.001	
Distance from forest edge	−0.0022	0.0001	<0.001		Distance from forest edge	−0.0006	0.0001	<0.001	

Distance from the Forest Edge Strongly Mediates the Effects of Species Diversity on AGB According to Mining Type

The structural equation models (SEM) showed good fits of the model to the data (CFI close to one and lower AIC values; Figure 2). SEMs showed that AGB was affected by the stand age, distance from the forest edge, and species diversity (Hill ^{0}D), but the significance and direction (+/−) of the relationship were dependent on the mining type (Figure 2).

Global SEM results, without differentiating the mining types, indicated that stand age ($\beta = 0.47$, $p < 0.001$) and species diversity had a positive direct effect ($\beta = 0.47$, $p < 0.001$) on AGB. Meanwhile, distance from the forest edge had no significant direct influence ($\beta = -0.10$, $p = 0.059$) on AGB but it showed a negative effect on species diversity (covariance = $-$ 0.46, $p < 0.001$), which ultimately had a direct effect on AGB. The covariance between stand age and species diversity was also significant (covariance = 0.22, $p < 0.001$) (Figure 2A).

In both types of mining, SEMs indicated that AGB increased significantly with increasing stand age, but this direct effect was a little stronger in heavy machinery mining ($\beta = 0.74$, $p < 0.001$) than in suction pumping mining ($\beta = 0.54$, $p < 0.001$). The effect of distance from the forest edge on AGB was significant and negative ($\beta = -0.711$ and $p < 0.001$) in heavy machinery forest stands and non-significant and negative ($\beta = -0.02$, $p = 0.670$) in suction pumping forest stands. Meanwhile, species diversity promoted AGB, but this direct effect was significantly stronger in suction pumping forest stands ($\beta = 0.43$, $p < 0.001$), whereas species diversity non-significantly declined AGB in heavy machinery forest stands ($\beta = -0.08$, $p = 0.496$). The covariance between distance from the forest edge and species diversity was also significant, but this effect was stronger in heavy machinery forest stands ($\beta = -0.74$, $p < 0.001$) than in suction pumping forest stands ($\beta = -0.32$, $p < 0.001$) (Figure 2B,C). Thus, the SEM results are consistent with the results of the analysis of variance and generalized linear models.

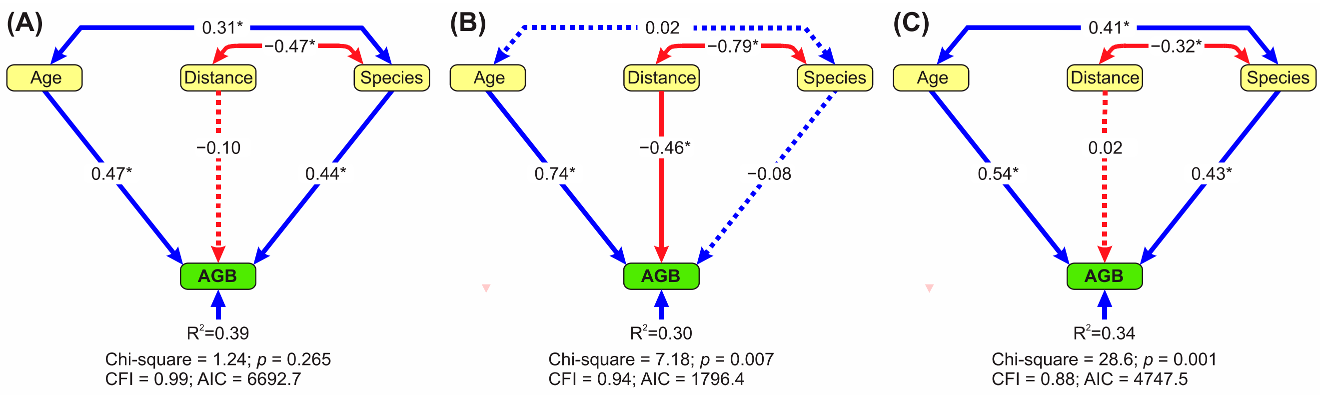

Figure 2. Results of structural equation models (SEM) showing the relationship between aboveground biomass (AGB), stand age (Age), distance from the forest edge (Distance), and number of species (Species) according to type of mining (heavy machinery and suction pumping). The blue arrows indicate positive effects, while the red arrows indicate negative effects. The dash and plain line types represent the non-significant ($p > 0.05$) and significant ($p < 0.05$) paths, respectively. For each path, a standardized regression coefficient value is shown. * Indicates the significant paths at 0.001. (**A**) = global SEM results, without differentiating by type of mining activities (heavy machinery and suction pumping); (**B**) = heavy machinery; and (**C**) = suction pumping.

3.2. Recovery of AGB, Tree Diversity and Forest Structure

Our results revealed that the AGB, tree height, DBH and effective number of species (Hill ^{0}D) increased with age of the stands. However, the pattern of recovery of these variables varied according to mining type. The pattern of AGB accumulation, recovery of DBH, height, and species diversity (Hill ^{0}D) showed a rapid increase in suction pumping mining forest stands in comparison to those of heavy machinery (Figures 3 and 4). High values of AGB and species were found in 20–25-year-old suction pumping stands; they were similar to reference forest stand values.

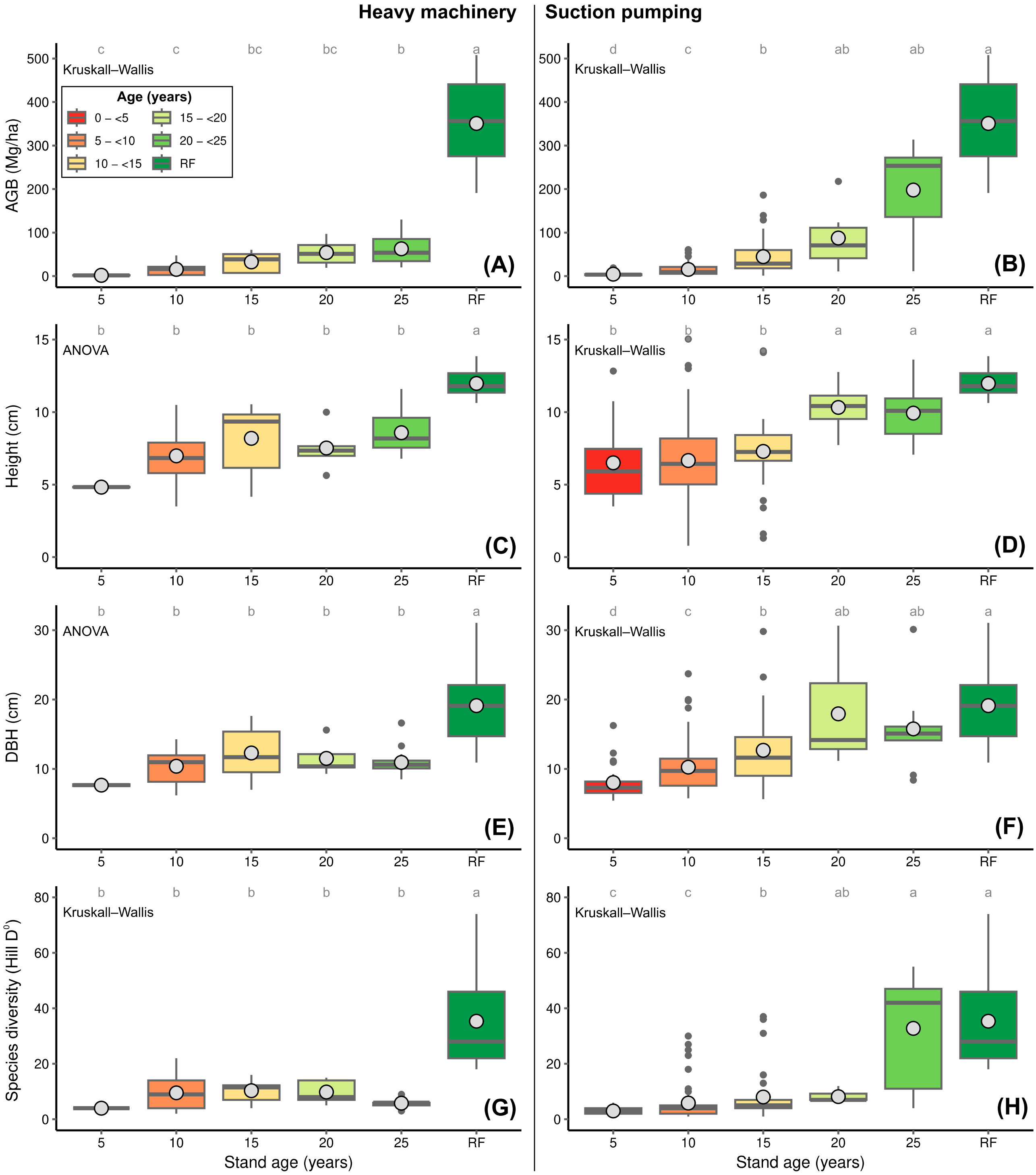

Figure 3. Comparison of AGB, species diversity and forest structure among forest plots in two types of mining activities (heavy machinery and suction pumping) according to five recovery age classes of natural regeneration and in reference forest of tree community across a chronosequence in degraded lands of the Peruvian Amazon. (**A**,**B**) AGB, (**C**,**D**) mean height, (**E**,**F**) mean DBH, and (**G**,**H**) species diversity (Hill ^{0}D). Different letters indicate significant differences among age classes for each variable (p < 0.05).

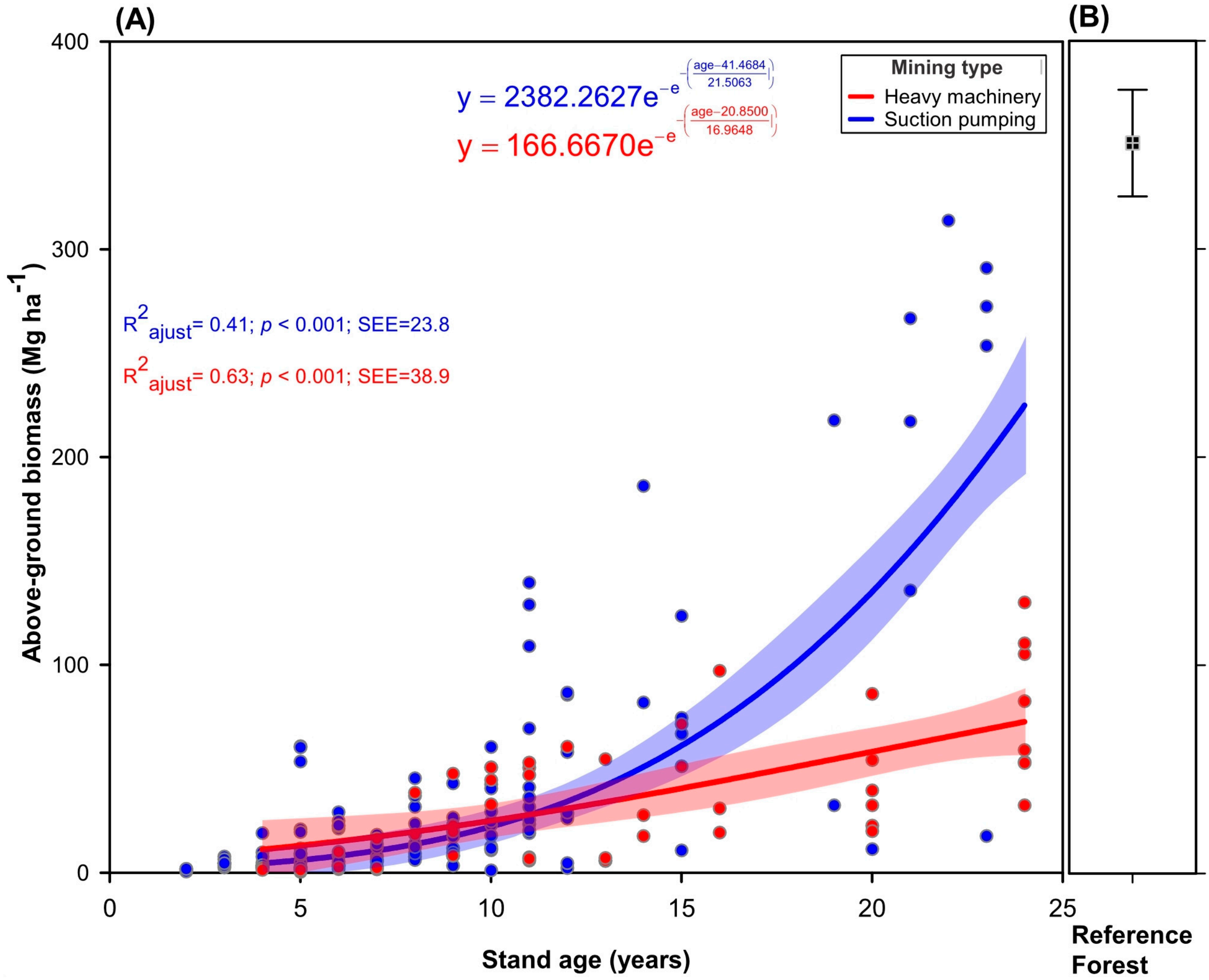

Figure 4. Relationship between aboveground biomass and stand age of tree community in two types of mining activities (heavy machinery and suction pumping) across a chronosequence in degraded lands of the Peruvian Amazon (**A**). Mean AGB (±standard error) of reference forests close to plots in degraded lands (**B**). SEE = standard error of estimate. The blue and red shading around each regression line represent the 95% confidence interval. The solid red circles represent data from a heavy machinery mining. The solid blue circles represent data from a suction pumping mining.

AGB increases recorded in heavy machinery stands (on average ranging from 1.9 to 62.9 Mg ha^{-1}) across the chronosequence were significantly lower (Kruskall–Wallis, $p < 0.001$) than that AGB accumulated in reference forests (351 ± 106 Mg ha^{-1}). However, in pumping mining stands, we found a rapid increase in the mean AGB, on average ranging from 3.8 to 115.7 Mg ha^{-1} depending upon the age of the succession (Figure 3). The AGBs of 20–25-year-old stands (198 ± 115 Mg ha^{-1}) were not significantly different (Kruskall–Wallis, $p > 0.05$) from the reference forest (351 ± 106 Mg ha^{-1}). On average, regenerating communities in pumping mining had reached 56% of reference forest AGB after 20 years, while in heavy machinery it was only 18% (Figure 3A,B). In our study, AGB recovery throughout a chronosequence (2–24-year-old) relative to reference forest AGB, varied from 3.3% to 89.6% (Figures 2 and 4). The resilience of AGB showed a high variation in potential AGB accumulation rates after 10 years of abandonment by goldmining and these patterns differed by mining type, with low rates in heavy machinery mining and high rates in suction pumping (Figure S2).

The vegetation structure (mean height and mean DBH) of secondary forest recovered at a much faster rate than species diversity and AGB, but it varied according to mining type. In >20-year-old regenerating communities in pumping mining stands it reached values of mean DBH and height slightly under and close to those of the reference forest (Kruskall–Wallis, Dun's post hoc test, $p < 0.05$) (Figure 3F). However, regenerating communities in heavy machinery were significantly lower than the reference forest (ANOVA, Bonferroni's post hoc test, $p < 0.05$) (Figure 3E). After 20 years, mean height and DBH in regenerating communities in pumping mining had reached 83% and 82% of reference forest, respectively, while in those of heavy machinery it was only 63% and 60%, respectively (Figure 3A,B).

On the other hand, on average, the number of species (Hill ^{0}D) per plot increased with category of stand age throughout the chronosequence, but the increase was higher in pumping mining stands than in heavy machinery. In pumping mining stands, Hill ^{0}D was highest in plots with a stand age greater than 20 years, and it was statistically indistinguishable from the mean Hill ^{0}D in the reference forest (Kruskall–Wallis, Dun's post hoc test, $p > 0.05$) (Figure 3H). In heavy machinery stands, significantly more Hill ^{0}D were recorded in reference forest than successional forest (Kruskall–Wallis, Dun's post hoc test, $p < 0.01$). There were no differences in Hill ^{0}D values among secondary forests (Kruskall–Wallis, Dun's post hoc test, $p > 0.05$) (Figure 3G).

3.3. Tree Species Dominance and Composition

A total of 303 tree species belonging to 167 genera and 61 families were recorded throughout all successional forests, for a total of 4699 woody trees across all plots. The dominance of tree species, genera, and families changed across the chronosequence and varied significantly according to mining type (Tables 3, S1 and S2). The five most abundant species were more dominant in regenerating areas after heavy machinery mining (IVI value of 27–73.9%) than in areas after suction pumping (IVI value of 59.1–77.5%). In early successional stages (<10 years old), pioneer species were dominant (IVI > 10% [72]). In regenerating areas after suction pumping mining, the dominant species were *Ochroma pyramidale*, *Cecropia engleriana,* and *Cecropia membranacea*, whereas in heavy machinery areas they were *Ochroma pyramidale*, *Trema micrantha*, *Piper aduncum,* and *Vismia macrophylla*. The IVI of pioneer species had a decreasing trend with the increase of stand age. In intermediate secondary succession (10 to <20-year-old), *Ficus insipida*, *Ochroma pyramidale,* and *Inga* spp. were considered dominants in areas of suction pumping mining, whereas in areas recovering from heavy machinery mining they were *Ochroma pyramidale*, *Piper aduncum*, *Miconia minutiflora,* and *Acalypha macrostachya*. On the other hand, in advanced secondary succession, the highest IVI of species differed between mining types. *Sapium marmieri*, *Erythrina poeppigiana,* and *Cecropia membranacea* were the most important species in suction pumping mining, whereas *Tachigali* spp., *Vismia* spp., and *Miconia* spp. were the most important species in heavy machinery. *Virola surinamensis*, *Astrocaryum murumuru*, *Guarea macrophylla*, *Brosimum lactescens,* and *Spondias mombin* were the dominant species in the reference forest plots (Table 3).

In both types of mining, Malvaceae was the dominant plant family in the early successional stages, followed by Urticaceae and Fabaceae in recovering areas of suction pumping, and by Cannabaceae, Fabaceae and Urticaceae in areas of heavy machinery mining. The IVI of Fabaceae and Malvaceae had increasing and decreasing trends, respectively, with the increase in stand age. In areas of heavy machinery mining, Melastomataceae had an increasing trend across the chronosequence. In both types of mining, Fabaceae was the most dominant species in the oldest secondary forest (20–25 years) as well as in the reference forest plots (Table S1).

In the early successional stages, however, Ochroma and Cecropia were the most dominant genera, followed by Trema, Piper, and Vismia in areas affected by heavy machinery mining, and by Andira, Inga, and Tessaria in areas of suction pumping. The IVI of Inga, Ficus, Guazuma, and Malvaceae rose with the increase of stand age in areas affected by suction pumping mining. Meanwhile, the IVI of Miconia, Vismia, and Apeiba increased with the increase of stand age in areas of heavy machinery mining (Table S2).

Table 3. Comparison of five species with the highest importance value index (IVI) of tree community by type of mining activities (heavy machinery and suction pumping) across a chronosequence in degraded lands and reference forest in the Peruvian Amazon.

Forest Stand Age (Years)	Mining Type			
	Suction Pumping		Heavy Machinery	
	Species	IVI (%)	Species	IVI (%)
(a) <5	*Ochroma pyramidale*	38.0	*Ochroma pyramidale*	35.3
	Cecropia engleriana	18.6	*Trema micrantha*	26.6
	Cecropia membranacea	10.2	*Piper aduncum*	10.9
	Trema micrantha	3.6	*Vismia macrophylla*	10.0
	Erythrina poeppigiana	3.4	*Coccoloba mollis*	8.6
(b) 5 to <10	*Ochroma pyramidale*	18.3	*Ochroma pyramidale*	36.1
	Cecropia membranacea	12.1	*Cecropia membranacea*	6.0
	Inga marginata	8.4	*Bauhinia sp1*	2.6
	Cecropia engleriana	6.5	*Erythrina ulei*	2.0
	Tessaria integrifolia	3.7	*Cecropia polystachya*	1.9
(c) 10 to <15	*Ficus insipida*	12.2	*Ochroma pyramidale*	9.9
	Ochroma pyramidale	12.2	*Cecropia engleriana*	4.3
	Cecropia engleriana	7.6	*Apeiba tibourbou*	3.4
	Inga sertulifera	7.3	*Piper aduncum*	2.8
	Cecropia membranacea	5.3	*Bellucia pentamera*	2.8
(d) 15 to <20	*Ochroma pyramidale*	25.8	*Piper aduncum*	10.0
	Ficus insipida	13.1	*Miconia minutiflora*	9.5
	Inga marginata	8.8	*Acalypha macrostachya*	9.2
	Inga thibaudiana	6.5	*Cecropia engleriana*	7.3
	Cecropia membranacea	6.4	*Apeiba membranacea*	5.9
(e) 20 to <25	*Sapium marmieri*	9.4	*Tachigali sp1*	26.2
	Erythrina poeppigiana	5.8	*Miconia tococa*	11.9
	Cecropia membranacea	5.3	*Vismia macrophylla*	10.0
	Pourouma cecropiifolia	3.3	*Vismia baccifera*	8.0
	Guazuma ulmifolia	3.2	*Miconia poeppigii*	7.4
(e) Reference forest	*Virola surinamensis*	3.0		
	Astrocaryum murumuru	2.8		
	Guarea macrophylla	2.4		
	Brosimum lactescens	2.2		
	Spondias mombin	2.1		

Using PERMANOVA in non-metric multidimensional scaling ordinations (nMDS), we found that the tree species composition of natural regeneration in abandoned mining lands differed significantly with mining type ($F = 1.07$, $p < 0.001$). The covariates stand age ($F = 1.12$, $p < 0.001$) and distance from forest edge ($F = 1.13$, $p < 0.001$) had an effect on similarity between assemblages of trees (Table 4), while we found an interactive effect between stand age × distance from forest edge, and between mining type × distance from forest edge (PERMANOVA, $p < 0.05$). But we did not see evidence of an interactive effect between stand age × mining type, and between stand age × distance from forest edge × mining type (PERMANOVA, $p > 0.05$) (Table 4). That would indicate the composition of natural regeneration of tree species at abandoned mining lands changed differently over time and was influenced by distance from the forest edge, and mining type.

PERMANOVA test showed differences in β diversity across mining type groups (Figure 5B). For categories of abandonment time, we only found significant differences in tree species composition between young (<5 years-old) and old stands (20–25 years-old) (Figure 5C).

Table 4. Results of analysis of variance (PERMANOVA) tests on natural regeneration of tree communities across a chronosequence in degraded lands of the Peruvian Amazon. Mining type was treated as fixed effects and stand age (years) and distance from the forest edge (m) were used as covariates. Significant *p*-values ($p < 0.05$) are shown in bold.

Source	df [1]	Sum of Squares	Pseudo-F	*p* (Permutation)
Age	1	5573.4	1.12	**<0.001**
Distance from forest edge (Dist)	1	5637.6	1.13	**<0.001**
Mining type (Min)	1	5300.7	1.07	**<0.001**
Age × Dist	1	5193.6	1.04	**<0.001**
Age × Min	1	5009.9	1.01	0.412
Dist × Min	1	5210.0	1.04	**<0.001**
Age × Dist × Min	1	5066.4	1.02	0.163
Residuals	172	845,150		

[1] df, degree of freedom.

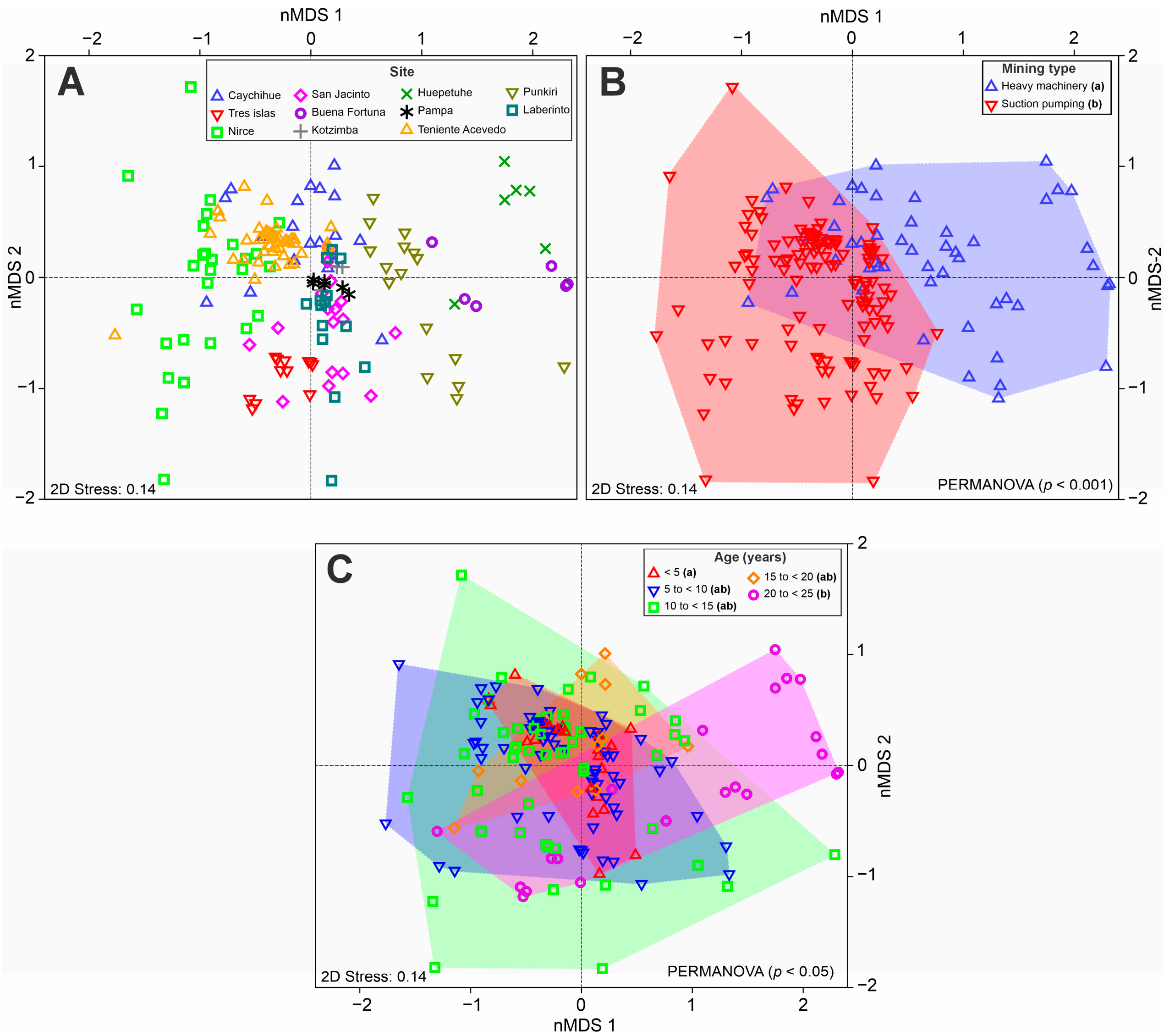

Figure 5. Non-metric multidimensional scaling ordinations (nMDS) of tree community composition (beta diversity) based on Chao–Jaccard similarity between natural regeneration across a chronosequence in degraded lands of the Peruvian Amazon. (**A**) Study sites, (**B**) type of mining, (**C**) stand age. In B and C, hulls overlaid for each variable. In each nMDS, different letters of the legend label indicate statistically significant differences according to pairwise PERMANOVA tests.

4. Discussion

Our study shows for the first time how the type of mining affects the resilience of structure, species diversity, and aboveground biomass of secondary forests following the abandonment of gold mining activity in the Southeastern Peruvian Amazon. To our knowledge, this field-based study provides the first assessment of how the type of mining can limit the recovery of AGB after mining. We sought to understand the relative importance of distance from the forest edge and species diversity in mediating the effects of different types of mining activities (heavy machinery and suction pumping) on AGB. Therefore, for effective restoration/reforestation strategies, these local site variables should be considered [73].

4.1. Effects of Mining Type, Stand Age, and Distance from the Forest on AGB

Our analysis shows that mining type, stand age, and distance from the forest edge had a significant effect on AGB. However, the influence of the distance from the forest edge could vary according to mining type. This is because the distance from the forest edge mediates the effects of species diversity on AGB. The negative effect of the distance from the forest edge was significantly greater in heavy machinery mining due to these lands being subject to high degrees of landscape fragmentation [74]. Meanwhile, in areas recovering from suction pumping mining, tree species diversity had a positive effect on AGB, as found previously in many studies [37,60,75]. This result indicates that these relationships are context-dependent [24], because the effect of the distance from the forest matters significantly in heavy machinery mining but not in suction pumping. This suggests that heavy machinery mining is severely impacting AGB resilience because the AGB accumulation may depend on stand forest age [76], land-use history [37], forest cover [30], soil properties [77,78], proportion of wind-dispersed species [79], and type and severity of disturbance [21,80]. In contrast, the small-scale disturbance caused by suction pumping mining and a relative short distance from a propagule source, in some sites of the study, promotes the establishment of species and increasing species diversity [41,81] and facilitating a faster AGB recovery [80,82] in areas recovering from suction pumping mining. This supports our results in SEM calculations and could explain why the AGB is higher in suction pumping mining forest stands. The positive relationship between AGB and tree species diversity found in suction pumping mining forest stands of the present study was reported by other studies in secondary forests [60,83,84] and old-growth forests [24,58,76,80,85]. Because of forest woody productivity, it is usually positively associated with tree species diversity [85]. Due to the coexistence of functionally different species, this may (1) increase resource partitioning of the environment, (2) enable positive plant–plant interactions and (3) improve growing conditions for establishment and growth of other species [79,83].

4.2. Recovery of AGB, Tree Diversity, and Forest Structure

Understanding the natural regeneration processes on degraded land after human activities is an essential goal of restoration ecology [78]. Our results from the study area support our initial hypothesis that the resilience of ecosystems degraded by mining in the Madre de Dios Amazon would be influenced by the type of mining, time of abandonment, and distance from the forest edge. This effect becomes clearer when we compare our results with reference ecosystems because AGB, effective number of species (Hill ^{0}D), as well as mean height and mean DBH of woody species of natural regeneration differed significantly from reference forests (except for suction pumping forest stands after 20-years of abandonment).

AGB strongly influences ecosystem processes [79] and tropical forests store significant quantities of AGB accumulated in woody plants [86]—64% of global forest AGB [87]. However, the expansion of deforestation and forest degradation in Madre de Dios persists [19,88], resulting in the emission of carbon into the atmosphere [16]. The mean AGB determined in 20–25 years of recovery, 198 ± 115 Mg ha^{-1} in areas of suction pumping mining and 45 ± 78 Mg ha^{-1} in areas recovering from heavy machinery mining in this study is less than the mean AGB reported for tropical Amazon forest from Madre de Dios (230–450 Mg ha^{-1}) [39,86,89]. This suggests a more rapid recovery of AGB in suction pumping mining forest stands in comparison to those of heavy machinery, because >20-year-old suction pumping forest stands store similar amounts of carbon as naturally regenerating forests on abandoned deforested lands (secondary forests from non-mining impacts) of similar age [4,90]. Furthermore, Sharma et al. [29] suggest that secondary forests can accumulate half of the AGB of reference forests within 30 years, which is consistent with our results in suction pumping mining (56% of recovery) but not with heavy machinery mining (18% of recovery). The rapid AGB recovery in suction pumping mining forest stands is consistent with those reported by other studies on tropical secondary forest succession [18,30]. Given that, after 20 years of abandonment, the average AGB accumulation reported by Oberleitner et al. [30] (52% of recovery) and Poorter et al. [18] (60% of recovery) agrees closely with our results (56% of recovery) (Figure S2). Although, there are very few studies of AGB recovery on secondary succession after mining in Amazonian forests, our results are consistent with those reported by Kalamandeen et al. [21] in Guyana, who found woody AGB recovery rates similar to secondary forests recovering from agriculture or pasture in early regenerating sites (2–4 years after abandonment) following gold mining activity. In this way, we found empirical evidence showing that regenerating forests after abandonment by mining activities could represent important carbon sequestration sinks, because secondary forests in the Amazon are a promising way to mitigate climate warming due to their higher productivity and carbon uptake compared to mature forests [4]. Furthermore, when tropical forests are disturbed, AGB is considered the main source of carbon emissions [80].

The rapid recovery of forest structure compared to AGB, species diversity, and composition have been widely reported by previous studies [41,60,79]. In our study, after 15 years, mean height and mean DBH of suction pumping forest stands recovered at a much faster rate than those recovering from heavy machinery mining—88% of DBH and 84% of height versus 58% of DBH and 67% of height, respectively. These differences are likely due to a higher species diversity in suction pumping forest stands, because a higher diversity of species can promote a greater development of the forest structure and increase aboveground light capture, where space and resources are used most effectively [91,92]. Previous studies reported that biomass growth can be negatively influenced by canopy structure [93,94] and forests with more biomass also have a more complex structure [79]. The slower recovery of forest structure generates a slow recovery of AGB in heavy machinery forest stands, because height and tree diameter variation are positively and strongly related to AGB [83]. This can be explained by the presence of low-diameter trees and a lower space optimization by co-occurring tree species in the canopy layer in heavy machinery forest, which impact negatively on biomass accumulation [58,83,91].

Similar to AGB, species diversity also increased with stand forest age [30], but it could vary according to the type of mining. Because only average species diversity in suction pumping forest stands (20–25-year-old) reached a similar level to reference forest at a slower pace than forest structure. These results indicate that heavy machinery mining may have a considerable negative effect on species diversity [21], because suction pumping mining forest stands harbor on average approximately two times more species than heavy machinery stands. Given that species diversity usually starts near zero with no woody plants, due to the elimination of vegetation cover [39,41,42] and severe soil degradation [20,43,44,54] by goldmining, our results highlight the lower impact of suction pumping mining on landscape structure, which promotes an increase over time as new species become established [79], and facilitates the faster recovery across the landscape [80]. The lower species diversity after mining abandonment may be explained by a higher dominance (IVI > 10, Table 3) or monodominance [30,95] of pioneer species in 0–5-year-old stands, due to higher tolerance of certain species to unfavorable soil conditions [95] generated by goldmining activities in the study area. Although monodominance in early secondary succession in Amazonian forests is rare [95], it is usually characterized by low tree species diversity and is linked with low soil fertility [95,96]. This agrees with our results (especially with respect to heavy machinery) because goldmining in the Peruvian Amazon generates extreme soil disturbance [41]. Soil from mine spoils after abandonment is characterized by significantly lower organic matter, cation exchange capacity, and clay content than the reference forests [44,47,54]. On the other hand, the decline in species diversity in the oldest forest stands of heavy machinery mining may be due to an increase in monodominance [96,97] (p.e. *Tachigali* spp., *Miconia* spp. and *Vismia* spp.) along the chronosequence, remoteness from existing forest edges [41,76,97], and a lower soil fertility than suction pumping [54]. In addition, different woody plant species can become monodominant due to smaller natural regeneration community size and may generate stochastic effects on species diversity [98]. As also reported by Oberleitner et al. [30] in tropical secondary forests in Costa Rica, they found an increase in monodominance by a few tree species in the later successional stage. This may explain why suction pumping forest stands have higher tree species diversity and AGB than those of heavy machinery [80].

4.3. Tree Species Dominance and Composition

In this study, we found a significant difference in species composition between the two types of mining activities. This may be related to differences in landscape fragmentation and proximity to the sources of propagules [82], as has been observed for other tropical forests [76,79] and secondary forests after mining in the Peruvian Amazon [41]. This difference in species composition and stand structure may have implications for biomass accumulation [30,99], due to the turnover of high wood density species [7,44,60] and the increase in species diversity [24,79,97].

The lower similarity in species composition (<20% in higher successional stages, Table S3) across the chronosequence suggests a slower recovery compared to those of AGB, species diversity and forest structure. This pattern has been observed for other tropical forests [37] and in secondary forests after mining in the Peruvian Amazon [20,39–41]. This highlights the need to promote active restoration strategies to establish both economically and ecologically important valuable native tree species [37]. In our study, the dynamics of the slow recovery of species follow the "initial floristic composition model" hypothesis [100], because the dominance (IVI) is relayed from one floristic group (species, genus or family) to another throughout the chronosequence [97]. This hypothesis states that pioneer species colonize early successional stages which remain for some decades [76], and soon they make suitable conditions for colonization by other species more typical of later successional stages [97]. A similar pattern was found in other secondary successions post mining in the Peruvian Amazon [41,41]. Species typical of the later successional stages are not present in the initial successional stages (<5 years of abandonment), and pioneer species are highly dominant in natural regeneration after goldmining activities.

High IVI values of tree species within a community show their ability to acclimate to their habitat and suggest a high tolerance for degraded environments [99]. Species such as *Ochroma pyramidale*, *Cecropia* spp., *Trema micrantha*, *Tessaria integrifolia*, *Vismia* spp., and *Inga* spp., may represent candidate species for more focused reforestation in degraded lands by gold mining in the study area. However, it could vary according to mining type and the establishment of different species in these severely degraded areas remains largely unstudied. Moreover, medium–long term reforestation/restoration studies in degraded lands by gold mining in the Peruvian Amazon are scarce, with only one study reported on reforestation after 20 years in areas degraded by heavy machinery in Madre de Dios [39]. Therefore, carefully planned field trials are essential for achieving the optimal selection of tree species for restoration or reforestation purposes [21].

Fabaceae is considered the most common family in tropical Amazonian forests [31] and the third largest family of angiosperms [101]. Due to symbiotic nitrogen fixation in Fabaceae species [102], they can drive early ecological succession [21,61] and they are important in secondary forest and successful restoration practices [103]. In our study, the dominance of Fabaceae is similar in advanced successional forest stands and in reference forest, *Inga* species capable of fixing nitrogen were dominant in both mining types. Similar results were found in other studies in degraded lands by gold mining in the Peruvian Amazon [20,39–41]. This is important because nitrogen fixers are known to drive biomass accumulation in recovering secondary forests [21].

4.4. Limitations and Suggestions for Future Research

This study has certain limitations. (1) We used cross-sectional data (chronosequence approach) and future studies need to be longitudinal to confirm the recovery rate of AGB, floristic attributes, and alpha and beta diversity. (2) We used small plots (0.01 to 0.25 ha), which could generate greater heterogeneity in forest structure and greater variation in biomass estimates [104] but not in β-diversity analysis. This is because in heterogeneous vegetation (as in the present study) with a high β-diversity ordination patterns are not sensitive to different plot sizes [105]. Despite these limitations, our results are consistent with other studies in secondary successions [21,41,41,76,79], and provide new insights for a deeper understanding of the natural regeneration recovery of degraded lands by goldmining in the Peruvian Amazon. In future studies, we will analyze differences in functional species traits [106] and in AGB by field measurements of wood density by mining type in chronosequences, in different edaphic conditions. Wood density may change across secondary succession due to changes in species composition; this is usually ignored and could affect AGB estimates [7]. Likewise, tropical forest carbon pools have been affected by soil nutrient availability [30]. This knowledge may be useful for effective strategies to restore forest cover and improve ecosystem services [38] on degraded lands through goldmining in the Peruvian Amazon.

5. Conclusions

Our results clearly showed the dynamics of AGB recovery across a secondary chronosequence after abandonment by goldmining, and the contrasting responses of AGB accumulation between two mining types. This is because the resilience of aboveground biomass, forest structure, and species diversity are affected by type of mining. Successional secondary forest recovery from suction pumping forest stands was more resilient than heavy machinery. After 20 years of abandonment, recovery of AGB, forest structure, and species diversity were higher in suction pumping forest stands than in those of heavy machinery. Moreover, the high AGB accumulation potential of the suction pumping forest stands could play a crucial role in carbon storage and global warming mitigation [107]. Our study disentangles the importance of environmental factors on forest recovery after mining. It helps us understand the resilience of highly degraded ecosystem of the Peruvian Amazon.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16040233/s1, Figure S1: Climate diagram of Puerto Maldonado meteorological station (1950–2023). Values shown in climate diagram correspond to the average month annual temperature (blue line), maximum temperature (red line), minimum temperature (green line), and the total month precipitation (gray bars). Orange line represent the dry season, when precipitation is lower than 100 mm per month; Figure S2: Relationship between aboveground biomass and stand age of tree community in two types of mining activities (heavy machinery and suction pumping) across a chronosequence in degraded lands of the Peruvian Amazon (A). Mean AGB (±standard error) of reference forests close to plots in degraded lands (B). SEE = standard error of estimate; Table S1: Comparison of five families with the highest importance value index (IVI) of tree community by type of mining activities (heavy machinery and suction pumping) across a chronosequence in de-graded lands and reference forest in the Peruvian Amazon; Table S2: Comparison of five genera with the highest importance value index (IVI) of tree community by type of mining activities (heavy machinery and suction pumping) across a chronosequence in degraded lands and reference forest in the Peruvian Amazon; Table S3: Average of floristic similarity (Chao–Jaccard) among forest plots in two types of mining activities (heavy machinery and suction pumping) according to five recovery age classes of natural regeneration and in reference forest of tree community across chronosequence in degraded lands of the Peruvian Amazon.

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