Natural Regeneration After Gold Mining in the Peruvian Amazon: Implications for Restoration of Tropical Forests

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Context: Gold mining is the most destructive activity in the natural forests of the Madre de Dios region in the southeastern Peruvian Amazon. Understanding the natural regeneration process of these degraded areas is necessary to develop forest restoration projects in such conditions.

Aims: We aimed to evaluate forest recovery and identify the successional and structure patterns of vegetation governing natural regeneration over time.

Methods: Structure, composition, richness, diversity, and successional status were evaluated in abandoned artisanal gold mine areas in Madre de Dios, southeastern Peru. Vegetation data were recorded in 61 plots of 250 m² established in five sites varying from 1 to 19 years of abandonment. Vegetation in abandoned areas was compared with six undisturbed forests evaluated in previous inventories.

Results: In the mining lands, tree density and basal area recovered quickly, while species richness and composition were slow. Forest recovery is an initial stage of transition from pioneer to early secondary species until at least 19 years after abandonment. The most abundant and frequent species were the fast-growing species Ochroma pyramidale and Cecropia engleri. These species could be considered potential candidates to promote restoration plans. Pioneer species represented 63% of the number of species in plots of 1–4 years, 57% in plots of 5–7 years, and 50% in plots of 8–19 years. Early and late secondary species represented 34 and 16%, respectively, of the number of species in plots of 8–19 years. Abandoned mining and reference plots present less than 5% of species in common.
INTRODUCTION

The southeastern region of Peru comprises one of the largest areas of preserved Amazon forest encompassing almost 30% of the total protected areas of the country (SERNANP, 2019). This region is recognized worldwide as part of the Tropical Andes Biodiversity Hotspot due to its high species diversity (Rodrigues, 2013). However, artisanal gold mining in the region is the principal driver of deforestation (Joshi et al., 2015). In the Madre de Dios region, gold mining-related deforestation was approximately 1,000 km² between 1984 and 2017 (Swenson et al., 2011; Asner et al., 2013; Caballero Espejo et al., 2018), and it was responsible for the highest annual deforestation rate since 2011, 80 km² year⁻¹ on average (Caballero Espejo et al., 2018). Forest loss appears as extensive wastelands with superficial soil layers removed, large mounds of sand, and artificial bodies of water (Mosquera et al., 2009; Kalamandeen et al., 2020). Long-lasting impacts also include mercury-polluted air, soil, and water (Scullion et al., 2014) that severely limits forest recovery (Mosquera et al., 2009).

Forest recovery strongly depends on the initial degree of degradation (Chazdon, 2008). In tropical forests, results from chronosequences analyzed in abandoned sites impacted by agricultural and pasture activities showed that regenerating forests can attain many of the structural characteristics and woody species richness comparable with old-growth forests within a few decades (Guariguata and Ostertag, 2001). In contrast, in gold mining areas, the recovery is slower and more complex and may not even occur because the impacts not only alter the vegetation but also soil characteristics (Peterson and Heemskerk, 2001; Lamb et al., 2005; Ren et al., 2007; Kalamandeen et al., 2020).

Old-growth or secondary forests surrounding the degraded areas function as important seed sources that facilitate forest recovery following mining (Rodrigues et al., 2004). Their spatial distribution as well as their proximity to degraded areas usually defines the composition and structure of natural regeneration (Pereira et al., 2013; de Rezende et al., 2015; Sloan et al., 2016). Nevertheless, management strategies are needed to promote forest recovery in highly degraded areas. Active restoration accelerates forest recovery in less resilient areas (Stanturf, 2005; Chazdon, 2008; Rodrigues et al., 2009).

In the Peruvian Amazon, most of the areas degraded by gold mining are surrounded by old-growth forests (Joshi et al., 2015), suggesting favorable landscape-scale conditions for natural regeneration (Chazdon and Guariguata, 2016). Although variation in secondary forest structure and composition following agriculture and pasture abandonment has been widely studied (Chazdon et al., 2007; Feldpausch et al., 2007; Norden et al., 2015), quantifying the structural and compositional parameters and the time of recovery in abandoned gold mining areas remains poorly known. Considering the urgent need to restore landscapes across the tropics, it is important to understand how vegetation recovery in such lands occurs over time.

In this study, we aimed to evaluate vegetation recovery to help develop restoration strategies of tropical forests under gold mining impacts. We analyzed (i) the relationship between vegetation structure status with the age of abandonment and (ii) the species richness, diversity, and successional patterns as a function of site age; and (iii) compared the floristic composition between abandoned and reference forests evaluated in previous inventories. We also sought to identify pioneer and secondary forest species to enrich or accelerate natural regeneration in abandoned gold mining areas.

MATERIALS AND METHODS

Study Areas

The study was conducted along the mining corridor of Madre de Dios Department, southeastern Peruvian Amazon (Figure 1). The corridor extends along the Madre de Dios River and Interoceanic Highway (PE-30). The forest is classified as seasonal tropical moist (Román-Dañobeytia et al., 2015; Dueñas and Garate, 2018). Mean annual rainfall is 2,300 mm and mean annual temperature is 27°C (SENAMHI, 2008).

Most of the artisanal gold miners are informal and/or illegal because they either lack the proper permits to operate or work outside authorized mining concessions (Scullion et al., 2014; Daley, 2016; EJAtlas, 2018). Miners primarily exploit riverbanks and primary forestlands (Damonte et al., 2013). Widespread tree mortality is observed in the abandoned mining areas, possibly due to sediment mobilization and anoxic or desiccating conditions and perhaps because of heavy metal contamination (Asner et al., 2013).

Five abandoned sites were located: “Tres Islas,” “Laberinto,” “La Pampa,” “Sarayacu,” and “Huepetuhe” of 220, 900, 2,000, 1,200, and 2,200 ha in area, respectively (Figure 1). Reference forests included the Universidad Nacional Amazonica de Madre de Dios (UNA) (Escalante, 2017; Carhuarupay, 2018), Inotawa (INO) (Mamani, 2012; Báez, 2014), Chonta (author’s database), and three plot metadata collected by Forest Plots.

Conclusion: Our results highlight a slow natural regeneration process in areas for up to 19 years after gold mining. Species from different successional statuses were identified as potential candidates for recovering vegetation in such areas. Our findings may have important implications for further research focusing on the ecological restoration in tropical forests severely degraded by gold mining.

Keywords: degraded area, forest disturbance, forest succession, Madre de Dios Region, natural regeneration, artisanal gold mining
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FIGURE 1 | Location of the study region including the abandoned gold mining plots (TRE, Tres Islas; LAB, Laberinto; SAR, Sarayacu; LAP, La Pampa; HUE, Huepetuhe) and undisturbed forest reference plots (UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico). The numbers within the images indicate the plot number.

Data Collection
Abandoned Mining Sites
Sixty-one plots of 250 m² (10 × 25 m) were randomly established in five mining sites (between 8 and 15 plots per site). The plot ages were determined by interviews and confirmed by examining satellite images between 1990 and 2016. In each plot, three size classes of woody species (all trees and shrubs) were recorded, identified, and measured, and botanical material was collected: small trees (10 cm diameter-at-breast-height, dbh), saplings (5–10 cm dbh), and seedlings (≥ 1 m height and < 5 cm dbh). The identification and classification was performed by botanists at the Alwyn Gentry Herbarium (Universidad Nacional Amazonica de Madre de Dios) and the San Marcos Herbarium (Universidad Nacional Mayor de San Marcos). The classification was based on the Angiosperm Phylogeny Group (Chase et al., 2016), and the scientific names were updated and standardized based on the data from Missouri Botanical Garden.1

Reference Forest
Table 1 shows the number and characteristics of plots in reference sites. In each plot, all trees ≥ 10 cm dbh were identified at the species level, and their height and dbh were measured. The species of abandoned mining and reference plots were also classified by their successional status (pioneer, early

1http://www.tropicos.org/
TABLE 1 | Plot characteristics in abandoned mining and reference sites.

| Abandoned mining sites (*) | Age since abandonment (years) | Total area (ha) |
|----------------------------|-----------------------------|-----------------|
|                            | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 10 | 15 | 19 |
| No. of plots, 250 m² (10 × 25 m) |     |     |     |     |     |     |     |     |     |     |     |
| Huepetuhe                  | 3  | 4  | 1  |     |     |     |     |     |     |     |     |
| La Pampa                   | 2  | 1  | 1  | 2  | 3  | 2  |     |     |     |     |     |
| Laberinto                  |     | 1  | 1  | 2  | 1  | 1  | 2  | 2  | 3  | 1  | 0.35|
| Sarayacu                   | 4  | 3  | 1  | 1  | 1  | 2  |     |     |     |     | 0.3 |
| Tres Islas                 | 5  | 7  | 3  |     |     |     |     |     |     |     | 0.375|

| Reference sites | No. of plots | Plot area | Total area (ha) | Date of evaluation | References |
|-----------------|--------------|-----------|-----------------|--------------------|-------------|
| UNA             | 32           | 10 × 100 m| 3.2             | 2017               | Escalante, 2017; Carhuarupay, 2018 |
| INO             | 4            | 10 × 500 m| 2               | 2012               | Mamani, 2012; Báez, 2014 |
| CHO             | 8            | 10 × 200 m| 1.6             | 2014               | Author’s database |
| TAM             | 9            | 100 × 100 m| 9              | 2008-2011          |             |
| LAS             | 1            | 100 × 100 m| 1              | 2008               | Lopez-Gonzalez et al., 2011 |
| CUZ             | 4            | 100 × 100 m| 4              | 2008               |             |

(*) Abandoned mining plot data include species information collected and described in Cutire and Ramirez (2017) and Sajami (2017). UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jadora Los Amigos; CUZ, Cuzco Amazonico.

Secondary, late secondary, or climax) based on a literature review of ecological studies in the Amazon rainforests (e.g., Gandolfi et al., 1995; Guariguata and Ostertag, 2001; Pitman et al., 2001; Gama et al., 2002; Souza et al., 2002; Da Silva et al., 2003; da Santos et al., 2004; do Amaral et al., 2009; Orrego and Zevallos, 2014; Dueñas and Garate, 2018).

Data Analysis

We classified plots into three groups by age of abandonment: 1–4, 5–7, and 8–19 years, with 22, 19, and 20 plots, respectively, based on a principal component analysis of mean diameter and height of seedlings, saplings, and small trees and the number of seedlings, saplings, small trees, pioneer, early secondary, and late secondary species by plot (Supplementary Figure 1). Three plots of La Pampa (two of 1 year and one of 2 years) did not have any individuals.

Linear regression analysis, plotting the age of site abandonment against species richness, basal area, and density of plants, for each successional status, was used to describe the pace of forest regeneration. Data correspond to 61 plot observations including pioneer, early secondary, and late secondary species. Analyses were performed in SAS Software, Version 9.4 (SAS Institute Inc, 2013).

Rank-abundance plots (Daly et al., 2018) were used to graphically depict the abundance distributions of species in each age group after mining, for each reference forest. For these analyses, log 10 transformation was performed. The relative abundance of species (%) by successional status was calculated. Shannon diversity index (H′) (Magurran, 1988) and the effective number of species (ENS) calculated as ENS = exp(H′) (Jost, 2006; Daly et al., 2018) were determined to compare plant communities among age groups and reference forests.

Rarefied species richness curves (Chazdon et al., 1998) were constructed to compare expected species for each age group after mining and reference old-growth forests. Ninety-five percent confidence intervals derived from 100 permutations were also calculated. Rarefaction curves are robust to estimate species richness, and they are recommended for unbalanced sampling design (Magurran, 1988).

The Importance Value Index (IVI) was also calculated (Lamprecht, 1990). The ranking of the highest 10 species according to their IVI was graphed for each site. Analyses were performed in Past 3.2.1 (Ryan et al., 2001) and Origin 2018 (OriginLab Corporation, 2018).

RESULTS

Forest Community Overview

We recorded 3,129 stems from 71 species of woody plants. Three plots (1 and 2 years since abandonment) from La Pampa did not have any individuals. In addition, 35 species were classified as pioneers, 23 as early secondary, and 13 as late secondary. Seventy percent of individuals corresponded to seedlings (61 species), 20% to saplings (43 species), and 10% to small trees (21 species).

In the reference plots, we recorded a total of 11,067 stems from 948 species of trees. Ninety-eight species were classified as pioneers, 314 as early secondary, 475 as late secondary, and 61 as climax.

Forest Structure, Species Richness, Diversity, and Successional Status Over Time

Total stem density was 2,155, 2,200, and 1,798 ind. ha⁻¹ for 1–4, 5–7, and 8–19 years after mining, respectively. Pioneers had the highest stem density in all age groups, representing 96, 89, and 69% of total stem density in plots of 1–4, 5–7, and 8–19 years post-abandonment, respectively. The relative density of early and late secondary species increased with abandonment age, from...
4.3% of total density in recently abandoned mines to 31% in the oldest plots. Small trees increased from 4 to 17% in plots of 1–4 and 8–19 years post-abandonment, respectively.

The pioneers *Ochroma pyramidale* and *Cecropia engleriana* showed the highest stem density across all ages. The stem density of *O. pyramidale* decreased with site age, from 1,235 ind. ha$^{-1}$ (1–4 years) and 998 ind. ha$^{-1}$ (5–7 years) to 328 ind. ha$^{-1}$ (8–19 years). The plots of 5–7 years presented the highest density of *C. engleriana*, 364 ind. ha$^{-1}$, while plots of 8–19 years presented the lowest, 132 ind. ha$^{-1}$.

Reference plots presented an average stem density of 551 ind. ha$^{-1}$ only for trees and small trees (>10 cm dbh). The species with the highest density were *Iriartea deltoidea*, *Pseudolmedia laevis*, and *Euterpe precatoria*.

Stem density, basal area, and species richness increased positively and significantly with increasing age of abandonment, and this pattern was consistent with the successional status. The exceptions were the density of pioneer and late secondary species that did not vary by increasing the abandonment age (Figure 2).

Steep curves for small trees, saplings, and seedlings at 1–4 years in the dominance–diversity curves graph indicate communities with high dominance of very few species in recently abandoned areas. Similar patterns were observed for saplings and small trees at 5–7 years (Supplementary Figure 2A). On the other hand, curves for seedlings at 5–7 and 8–19 years show a relative uniformity in the distribution of individuals among the species of the community. These results indicate a more diverse species assemblage for seedlings and saplings.

Rarefied species richness (30 individuals) ranged from 8 to 10 species in abandonment plots (Supplementary Figure 2C) and 23–25 species in reference plots (Supplementary Figure 2D). The ENS and $H^\prime$ show that the diversity in all size classes increased positively with abandonment age, although diversity is lower compared with the reference plots (Table 2).

The plant community across abandoned plots was dominated by pioneer species followed by early secondary species. Late secondary species were slightly proportionally higher in plots of 8–19 years of abandonment compared with the other plot.

| Age of abandonment (years) | Pioneer | Early secondary | Late secondary |
|----------------------------|---------|-----------------|---------------|
| Density (ind. ha$^{-1}$)   | Fit     | 95% Confidence Limits | 95% Prediction Limits |
| MSE 6.8866 R-Square 0.015 Adj R-Square -0.002 p 0.3478 | | | |
| MSE 83.303 R-Square 0.193 Adj R-Square 0.1793 p 0.0004 | | | |
| MSE 54.986 R-Square 0.038 Adj R-Square 0.0189 p 0.1476 | | | |
| Basal area (m$^2$ ha$^{-1}$) | Fit     | 95% Confidence Limits | 95% Prediction Limits |
| MSE 0.9363 R-Square 0.0677 Adj R-Square 0.0519 p 0.0425 | | | |
| MSE 3.227 R-Square 0.2075 Adj R-Square 0.2499 p <0.0001 | | | |
| MSE 0.4244 R-Square 0.085 Adj R-Square 0.0695 p 0.0286 | | | |
| Species richness | Fit     | 95% Confidence Limits | 95% Prediction Limits |
| MSE 5.6363 R-Square 0.1805 Adj R-Square 0.1666 p <0.0001 | | | |
| MSE 2.9754 R-Square 0.2385 Adj R-Square 0.246 p <0.0001 | | | |
| MSE 0.5717 R-Square 0.0896 Adj R-Square 0.0741 p 0.0191 | | | |
TABLE 2 | Richness and diversity for the abandoned gold mining and reference forests plots in Madre de Dios, southeastern Peru.

| ENS | H |
|-----|---|
| Abandoned gold mining plots | |
| 1–4 years | Seeds | 6 | 1.79 |
| | Saplings | 2 | 0.59 |
| | Small trees | 1 | 0.28 |
| 5–7 years | Seeds | 12 | 2.44 |
| | Saplings | 7 | 1.94 |
| | Small trees | 4 | 1.32 |
| 8–19 years | Seeds | 19 | 2.92 |
| | Saplings | 14 | 2.86 |
| | Small trees | 9 | 2.24 |
| Reference forests | CHO | 110 | 4.70 |
| | CUZ | 91 | 4.81 |
| | INO | 95 | 4.55 |
| | LAS | 74 | 4.30 |
| | TAM | 162 | 5.09 |
| | UNA | 98 | 4.58 |

ENS, effective number of species; H, Shannon index; UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico.

ages (Figure 3A). The plant community in reference plots was dominated by early and late secondary species and a small set of pioneer and climax species (Figure 3B).

**Forest Composition**

The IVI shows that *O. pyramidale* and *C. englerianna* are the dominant species across all abandoned plots, ages, and size classes (Supplementary Figure 3A). Furthermore, other pioneer species such as *Piper* sp. (seedlings), *Schizolobium parahyba* (saplings), *Guazuma crinita*, and *Senna silvestris* (small trees) presented high IVI in plots of 8–19 years of abandonment. *Inga thibaudiana* was the only non-pioneer species ranked among the 10 highest IVI in areas 5–7 and 8–19 years of abandonment.

In reference plots, the IVI shows that *I. deltoidea*, *E. precatoria*, *P. laevis*, and *Bertholletia excelsa* are the most important species in almost all areas. Forty-five, 40, 10, and 2% of the species in the reference plots corresponded to late secondary, early secondary, climax, and pioneer, respectively (Supplementary Figure 3B).

**Shared Taxa**

Plots younger than 7 years post-abandonment shared 29% of similarity (Supplementary Figure 3). This pattern was observed in both La Pampa and Huepetuhe plots. The oldest sites, Laberinto and Tres Islas, shared 35% of the species. Abandoned mining and reference plots presented less than 5% of species in common. *Ficus maxima*, *Jacaranda copaia*, *S. parahyba*, *Terminalia oblenga*, *Trema micrantha*, *G. crinita*, *O. pyramidale*, *Cecropia* sp., *Inga* sp., *Piper* sp., and *Triplaris* sp. were the main species observed in both abandoned and reference plots. Some of them were recorded in the oldest abandoned mining plots (Laberinto and Tres Islas) as seedlings and saplings.

**DISCUSSION**

**Forest Recovery Following Gold Mining**

Considering the concerns about the recovery of vegetation in abandoned gold mining lands, we show that structural and compositional parameters presented different patterns of recovery, likely reflecting the biotic and abiotic local variations in the sites and historical land-use changes. Our results point out faster recovery of forest structure than recovery of species composition and species diversity. This is a relevant finding since in some cases the recovery of forest structure following gold mining in Amazonian forests is close to zero or extremely slow, as in Suriname (Peterson and Heemskerk, 2001) or Guyana (Kalamandeen et al., 2020).

The density and basal area of early secondary species increased with age since abandonment. Contrary to expected, the stem density of pioneers and late secondary species did not vary with plot age. Considering that basal area represents a conservative estimate of the total biomass (Gilman et al., 2016), this has accumulated rapidly in most plots and showed a positive increase as the plot age increased. These results highlight the value of naturally regenerating sites for promoting the provision of ecosystem services related to carbon storage and sequestration (Rozendaal et al., 2019). Other studies argue that carbon storage from regenerating forests may not reach levels of old-growth forests until many decades later (Denslow and Guzman, 2000; Mascaro et al., 2012).

Although species richness increased positively with abandonment age, it represented only 9–19% of that reported in reference forests. This result has been also described in other studies across the Amazon Basin (e.g., Lozano Baez, 2013; Valois-Cuesta and Martinez-Ruiz, 2017; Kalamandeen et al., 2020). Changes promoted by mining activities are even more intense than other human-induced land conversions such as agriculture and pastures (Fujisaka et al., 2000; Guariguata and Ostertag, 2001).

In the oldest abandoned plots, pioneer species had four times the stem density and almost twice the richness relative to early secondary species. These values were even higher when compared with late secondary species. Despite the dominance of the pioneers, the richness, basal area, and stem density of the early and late secondary species increased over time. Consistent with previous studies (Peterson and Heemskerk, 2001; Rozendaal et al., 2019), these floristic and structural changes indicate a transition from pioneer to early secondary species at least until 19 years after abandonment. The dominance of early–late secondary species can take a few more decades (Rodrigues et al., 2004; Van Breugel et al., 2013), whereas the progression of secondary into old-growth forest can take centuries (Peterson and Heemskerk, 2001; Sharma and Chaudhry, 2018; Rozendaal et al., 2019).

**Factors Influencing Forest Recovery Patterns**

The high abundance of pioneer species can be related to their seed dispersal strategies (Rozendaal et al., 2019) and their fast growth
Implications to Forest Restoration

The slow pace of natural regeneration observed after 19 years of mining abandonment suggests the need for active restoration strategies with soil reclamation efforts to accelerate forest recovery. The combination of strategies can assist the restocking of transitional succession species speeding up the succession process (Evans et al., 2013; Román-Dañobeytia et al., 2015; Orozco-Aceves et al., 2017). In the southeastern Peruvian Amazon, however, considering that active restoration with soil reclamation costs $2,100–3,500 US$ ha$^{-1}$ during the first year of activity (Román-Dañobeytia et al., 2015) and that the areas degraded by gold mining sum up to 80,000 ha, only during 2007–2017 (Caballero Espejo et al., 2018), this strategy imposes financial challenges. Therefore, it is necessary to evaluate the relative effectiveness of different restoration strategies, ranging from passive (e.g., natural regeneration) to more intensive ones (e.g., mixed plantations of native species with soil reclamation). In older sites, natural regeneration followed by enrichment with late-successional species could further accelerate the successional process.

Despite not formally testing the tolerance of specific species to soil conditions, we observed that several tree taxa were found continuously at high densities despite the extensive soil disturbance. *O. pyramidale* and *C. engleriana* colonized and dominated areas 19 years after abandonment, which could have created a favorable structure for the establishment of early secondary species in older areas, providing shade and contributing to organic matter (Mesquita et al., 2001). Both could be key species in facilitating forest succession in recently abandoned mining lands. *G. crinita*, *S. parahyba*, and *C. spruceanum*, pioneer species co-dominating the oldest areas, could also be considered as potential species to be used in restoration strategies, as they have timber value (Reynel et al., 2003). Tree plantations using timber species have been recognized as a cost-effective alternative to convince landowners to recover or catalyze successional processes in degraded lands (Lamb et al., 2005; Rodrigues et al., 2009). *I. thibaudiana*, a non-pioneer species found in abandoned 5-year-old plots (Supplementary Figure 3A), commonly grows under broad environmental conditions (Schierenbeck et al., 1997), and similar to other *Inga* spp., it recovers and enriches soils through nitrogen fixation (do Vale et al., 2014; UICN, 2019).

CONCLUSION

After gold mining in Madre de Dios, forests regenerating demonstrated a high potential for biomass recovery throughout the regeneration process and a high conservation value in degraded landscapes. Stimulating their natural regeneration and testing some restoration strategies (e.g., soil reclamation, species enrichment) to accelerate forest recovery in such areas

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**Table 1**

| Species | Reference Forests | Abandoned Mining Plots |
|---------|-------------------|------------------------|
| *O. pyramidale* | Common in natural regeneration | Present in all plots |
| *C. spruceanum* | Pioneer species | Present in all plots |
| *G. crinita* | Early secondary species | Present in all plots |
| *S. parahyba* | Pioneer species | Present in all plots |

(Kalamandeen et al., 2020), while the low abundance of early and late secondary species could be due to soil removal (e.g., tailing ponds and mining pits) (Peterson and Heemskerk, 2001; Román-Dañobeytia et al., 2015; Kalamandeen et al., 2020).

However, we observed improvements in some soil characteristics over time (% sand and nutrients) (Supplementary Table 1), although the soil quality remained below that of reference forests. Despite the severe impacts on soil conditions, the complexity of the vegetation increased slightly with the abandonment age. The surrounding old-growth forests can probably function as a continuous source of seeds and contribute to increasing diversity over time (Fujisaka et al., 2000; Rodrigues et al., 2004).

**Forest Composition in Abandoned Gold Mining Areas**

Plant composition in almost all abandoned plots and plant size classes show that the dominant species are the fast-growing *O. pyramidale* and *C. engleriana*. Similarly, abandoned fallows in central-eastern Peru are dominated by *T. micrantha* and *Cecropia membranacea* (Fujisaka et al., 2000). In many other degraded lands across the Amazon basin, the presence of *Cecropia* spp. is common in natural regeneration but *O. pyramidale* (Mesquita, 2000; Mesquita et al., 2001; Rodrigues et al., 2004; Kalamandeen et al., 2020) is not, even though *O. pyramidale* is naturally distributed in these areas (ITTO, 2019).

The composition of the surrounding forests plays an important factor in driving the floristic composition of the plots. *O. pyramidale* and *Cecropia* spp. are abundant in riverbanks in the Madre de Dios region, and *G. crinita*, *S. parahyba*, and *Calycophyllum spruceanum* are common species in secondary forests and even in primary forests of this region (Gentry, 1982; Phillips and Gentry, 1993; Reynel et al., 2003; Dueñas and Garate, 2018).
are fundamental to complement the biodiversity conservation provided by surrounding reference forests.

**DATA AVAILABILITY STATEMENT**

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

**AUTHOR CONTRIBUTIONS**

RC-L, DOR, FF, JPV, PZP JM-P, and DR conceived the research idea. RC-L, JPV, and PZP collected data. RC-L, DOR, and DR performed statistical analyses and wrote the manuscript, with contributions from FF, JPV, PZP, and JM-P. JM-P and PZP made the determination of successional status of all plant species of the areas. All authors discussed the results, commented, and approved the manuscript.

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**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.594627/full#supplementary-material

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