Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

PROGRAMA DE DOCTORADO EN
Conservación y Uso Sostenible de Sistemas Forestales

TESIS DOCTORAL:

INFLUENCIA DE LA MINERÍA Y FACTORES AMBIENTALES SOBRE LA BIOMASA, PRODUCTIVIDAD Y RECICLAJE DE NUTRIENTES EN BOSQUES TROPICALES DEL CHOCÓ BIOGEOGRÁFICO.

Presentada por **David Fernando Pérez Abadía** para optar al grado de
Doctor/a por la Universidad de Valladolid

Dirigida por:
Dr. José María Del Arco Montero
Dr. Harley Quinto Mosquera

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Agradecimientos

Detrás de la elaboración de esta tesis, existe el invaluable apoyo de muchas personas que han sido imprescindibles a lo largo de este camino.

En primer lugar, expreso mi profunda gratitud a los profesores Harley Quinto Mosquera y José María Del Arco (Chema). Del profesor Quinto Mosquera aprendí sobre el pragmatismo científico y una admirable dedicación monástica para compaginar la investigación y la docencia. El profesor Chema, con su amplia dedicación y apoyo académico, me acogió generosamente en esta etapa del doctorado. A ambos, mi eterna gratitud por guiarme hacia este logro y prepararme para los nuevos retos que están por venir.

Asimismo, quiero destacar la guía y el apoyo inconmensurable del profesor Joaquín Navarro Hevia durante mis cursos doctorales. Su orientación como director y tutor fue un pilar fundamental en este proceso, incluso allanándome el camino antes de gozar de su merecida jubilación.

A mis compañeros y amigos de curso en la Universidad de Valladolid: Maritza Suárez, José Harvey Galvis, Eric Cudjoe y Andrés Armijos, entre otros.

A Juliana, Alexandre y Alisson de la universidad Federal de Ceará en Brasil. agradezco de corazón su compañía y apoyo en los diferentes estadios del doctorado.

También a mis amigos y colegas de la Universidad Tecnológica del Chocó: Jhon Fredy Asprilla, Miller Marmolejo, Jesús David Ponce, George Chaves y Harry Copete, Nicolas Valencia, entre muchos otros, quienes me brindaron no sólo respaldo académico, sino también ánimo en los momentos necesarios.

Extiendo mi agradecimiento a la Universidad Tecnológica del Chocó, ASPU-UTCH y a la Fundación Carolina, instituciones cuyo apoyo ha sido clave para alcanzar este objetivo.

Finalmente, mis más profundos agradecimientos a mi familia: a mi madre Amanda Abadía, mis hermanos Luz Yadira, Pedro Francisco, Jairo Daniel, Dora Marina. A mis vecinos y amigos de vida, por estar siempre presentes y darme su apoyo incondicional. A mis hijos, José Gabriel y Juan Diego, quienes son la mayor fuente de

inspiración en mi vida. Espero que el camino de todos continúe siendo tan exitoso como el que hemos recorrido juntos.

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Índice

Introducción ... 1

Hipótesis de investigación. ... 5

Hipótesis alternativa 1: ... 6

Hipótesis alternativa 2: ... 6

Hipótesis alternativa 3: ... 6

Preguntas de investigación ... 7

Objetivos ... 9

Objetivo general ... 10

Objetivos específicos ... 10

Metodología ... 11

1.Área de estudio ... 12

2. Diseño experimental ... 12

3. Medición de parámetros físicos y químicos del suelo ... 12

4. Medición de la producción de hojarasca ... 13

Análisis de datos. ... 17

Resultados ... 19

Artículo 1: Biomasa Aérea y Factores Ambientales ... 20

Artículo 2: Ciclaje de Nutrientes en Bosques Afectados por la Minería ... 21

Artículo 3: Productividad Primaria Neta y Fertilidad del Suelo ... 22

Artículo 1 ... 24

Influence of Environmental Factors on the Aboveground Biomass of Mature and Postmining Forests in Chocó ... 24

Abstract ... 24

Introduction ... 25

Materials and Methods ... 27

Results 33

Discussion 39

Supplementary Materials 43

References 44

Artículo 2 49

Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian. Pacific. 49

Abstract. 49

Introduction 50

Materials And Methods 53

Diameters and height of trees 54

Results 57

Discussion 58

Conclusions 67

Acknowledgements 68

References 68

ARTÍCULO 3 79

Influence of Mining on Nutrient Cycling in the Tropical Rain Forests of the Colombian Pacific. 79

Abstract. 79

Introduction 80

Materials and Methods 82

Methods 84

Results 87

Discussion 95

Conclusions 107

References 109
Conclusiones 119
Bibliografía 123

Tabla de figuras

Figura 1 Mapa de Distribución de parcelas permanentes 14
FIgura 2 Study area, Chocó, Colombia 30
FIgura 3 Principal component analysis (PCA) of ecological variables 38
FIgura 4 Linear regressions of above ground tree net primary productivity (NPP) 62
FIgura 5 Effects of mining on soil nutrient content in rainforests of the Colombian Pacific 89
FIgura 6 Effects of mining 91
FIgura 7 Effects of mining on foliar nutrients in tropical rain forests of the Colombian Pacific 93
FIgura 8 Effects of mining on foliar nutrients in tropical rain forests of the Colombian Pacific 94
FIgura 9 Effects of mining on nutrient use efficiency (NUE) in tropycal rain forests of the Colombian Pacific 95

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Tabla de gráficas

Tabla 1 Structural, ecological, and edaphic characteristics of the primary and recovering (from abandoned mines) fotests evaluated in Chocó 28

Tabla 2 Aboveground biomass 35

Table 3 Analysis of variance for aboveground biomass of trees as a function of structural and ecological variables for primary forests and abandoned mines of Chocó biogeographic region. Where R^2 = 41.3%, R^2 (adjusted) = 38.1%. 36

Tabla 4 Analysis of variance and multiple regression for aboveground tree biomass as a function of structural and ecological variables for primary forests in Chocó. 37

Tabla 5 Results of analysis of variance and multiple regressions for aboveground tree biomass as a function of structural and ecological variables for forested abandoned mine areas in Chocó... 37

Tabla 6 Aboveground biomass and wood net primary productivity of two post minigng forests in the Colombian 58

Tabla 7Analysis of variance of wood net primary productivity based on the soil physicochemical properties 59

Tabla 8 Spearman correlations of carbon sequestration and physichemical properties of post mining forests in the Colombian Pacific 60

Introducción

Los bosques tropicales son reconocidos como los ecosistemas terrestres más importantes del planeta debido a su alta biodiversidad, tasas de endemismo y capacidad para secuestrar carbono; lo cual, es vital en el equilibrio de carbono y la mitigación del cambio climático global (Pan et al., 2011). Este importante papel ha generado un creciente interés en la evaluación de la productividad primaria neta (PPN) de estos bosques y los factores que la determinan, tanto ambientales como antrópicos (Phillips et al., 1998; Malhi et al., 2011).

Los bosques tropicales son importantes sumideros de carbono, ya que almacenan una parte sustancial del carbono terrestre del planeta en su biomasa. Esta capacidad de secuestrar carbono desempeña un papel crucial en la mitigación del cambio climático al reducir la cantidad de dióxido de carbono en la atmósfera. Los estudios han demostrado que los bosques tropicales contienen el 25% del carbono terrestre y son responsables del 34% de la productividad primaria bruta (Vincent, 2019; Bonan, 2008; Beer et al., 2010). Además, a la mayoría de estos ecosistemas se les considera como puntos calientes de biodiversidad (*Hotspot*), que sustentan una inmensa variedad de especies de fauna y flora, que no se encuentran en ningún otro ecosistema (Myers et al., 2000). Esta diversidad de especies contribuye a las funciones ecológicas y a los servicios ecosistémicos, incluidos la captura de carbono y el reciclaje de nutrientes (Vincent, 2019).

Estos ecosistemas son fundamentales para los ciclos globales del carbono y la regulación del clima debido a su alta productividad primaria (Lu et al., 2024). Además, se encuentran entre los más productivos de la tierra, y contribuyen a la productividad primaria bruta terrestre dada su densa vegetación y rápida acumulación de biomasa (Beer et al., 2010; Bonan, 2008). El rápido ciclo de nutrientes, en particular del carbono, se ve facilitado por la alta biodiversidad de estos bosques (Montagnini y Jordan 2002). Esta biodiversidad, no solo sustenta varios niveles tróficos, sino que también mejora la absorción y el reciclaje de nutrientes, que son cruciales para mantener la salud y la productividad de estos ecosistemas. Las complejas interrelaciones entre las especies de los bosques tropicales impulsan el ciclo eficiente de los nutrientes y el flujo de energía, lo que resalta la importancia ecológica de la biodiversidad para mantener las funciones de los ecosistemas (Hooper et al., 2005; Loreau y Hector, 2001).

Según Montagnini y Jordan (2005), los bosques tropicales se caracterizan por presentar una significativa biomasa aérea debido a la densidad y diversidad de su vegetación, incluyendo una gran cantidad de árboles altos y frondosos. Además, poseen una productividad primaria neta muy alta debido en gran medida a la eficiencia en absorción y ciclaje de nutrientes, a pesar de tener suelos infértiles y pobres en nutrientes (Cleveland et al., 2003, Whitmore, 1998; Lu et al., 2024), y a las condiciones climáticas favorables, como la alta temperatura, la abundante precipitación y la disponibilidad de luz solar, que permiten un crecimiento vegetal rápido y continuo durante todo el año (Schuur 2003, Clark *et al.,* 2001a). Igualmente, en estos bosques la descomposición de la hojarasca y materia orgánica es rápida debido a las altas temperaturas y la humedad constante, que favorecen la actividad de los descomponedores como bacterias y hongos (Nye, 1961; Mori et al., 2022; Olson, 1963). Este proceso es crucial para el reciclaje de nutrientes en el suelo, y es muy eficiente porque permite la liberación de los nutrientes desde la hojarasca, que son rápidamente absorbidos por las raíces de las plantas, manteniendo la fertilidad del suelo y la alta productividad del ecosistema (Mori et al., 2022; Walker y Syers, 1976). En consecuencia, estas características hacen que los bosques tropicales sean ecosistemas altamente productivos, dinámicos y biodiversos (Montagnini y Jordan 2005).

Sin embargo, estos importantes procesos ecológicos que se presentan en los trópicos, como productividad y reciclaje de nutrientes, están siendo fuertemente afectados por actividades económicas como la deforestación, tala selectiva, ganadería, cultivos (lícitos e ilícitos), expansión de la frontera agrícola, sobreexplotación de especies, crecimiento en infraestructura, construcción de vías terrestres, minería a cielo abierto, entre otros (Montagnini y Jordan 2005).

Particularmente, la minería a cielo abierto afecta de forma considerable a los bosques tropicales (Primack y Vidal 2019); en efecto, dicha actividad tiene impactos significativos sobre estos ecosistemas; entre los cuales, se puede mencionar la deforestación directa causada por la eliminación de la cobertura vegetal para desarrollar la infraestructura minera y los sitios de extracción (Primack y Vidal 2019); lo que genera una pérdida de hábitat para especies de fauna y flora (Sonter et al., 2017; Laurance, 2015). Además, la minería produce fragmentación del bosque posterior a la deforestación, que puede aislar las poblaciones de especies, reduciendo la diversidad genética y aumentando su vulnerabilidad a enfermedades y cambios ambientales (Haddad et al, 2015).

La minería ha generado impactos severos en los bosques tropicales, en términos de deforestación, degradación, contaminación del agua y el suelo, fragmentación de los ecosistemas, disminución de la biomasa y PPN, reducción de la capacidad para regular el clima global, destrucción de hábitats y pérdida de biodiversidad (Pratiwi et al., 2021, Giljum et al. 2022, Primack y Vidal 2019). Entre los años 2000 y 2019, la expansión de la minería industrial provocó una pérdida directa de 3264 km² de bosque tropical, concentrándose el 80% de esta deforestación en solo cuatro países: Indonesia, Brasil, Ghana y Surinam (Primack y Vidal 2019). Particularmente, Indonesia lidera esta lista con el 58,2% del total, impulsado por la extracción de carbón en Kalimantan, Borneo; seguido por la deforestación en Brasil, aunque con menor proporción sigue siendo significativa, en especial en su Amazonía, donde la minería también afecta áreas protegidas (Primack y Vidal 2019). Todo esto, evidencia el impacto negativo de esta actividad económica sobre los ecosistemas naturales.

Particularmente, en regiones como el Pacífico colombiano, la minería a cielo abierto ha sido una de las principales causas de degradación forestal, afectando negativamente el ciclo de nutrientes y la dinámica del ecosistema (ELAW, 2010; Valois, 2016; Quinto et al., 2022). Esta actividad, genera la destrucción de horizontes del suelo, cambia la textura edáfica, disminuye la materia orgánica (MO), modifica el microclima del ecosistema, contamina ríos, afecta la vegetación y reduce la biodiversidad, lo que altera el funcionamiento del ecosistema y el reciclaje de nutrientes (Ramírez y Ledezma 2007; Ángel et al., 2019). Se estima que, la minería ha degradado anualmente más de 360 mil hectáreas de bosque natural en los últimos años (Ramírez y Rangel, 2019). Hasta 2015, se otorgaron licencias para la explotación de más de 300 mil hectáreas de bosque natural, evidenciando un impacto significativo en la vegetación y los nutrientes del suelo (Ángel et al., 2019). Sin embargo, poco se conoce sobre los posibles efectos de la minería sobre la biomasa aérea, PPN y reciclaje de nutrientes de bosques pluviales tropicales, lo que muestra la necesidad de investigaciones que evalúen esta influencia.

En bosques pluviales tropicales del Chocó biogeográfico se ha registrado una biomasa aérea de entre 100-200 toneladas por hectárea, influenciada por factores como fertilidad, estructura, diversidad, entre otros (Quinto y Moreno 2011, Faber-Langendoen y Gentry, 1991), a pesar de que presentan suelos ácidos y pobres en nutrientes (Quinto y Moreno 2016, Quinto et al., 2022). Asimismo, se ha cuantificado una PPN de entre 23.7 y 24.2 ton/ha/año, determinada por factores como contenido de nutrientes, textura, entre otros (Quinto y Moreno 2017). Mientras que, en términos del reciclaje de nutrientes se ha presentado una tasa de descomposición de hojarasca de entre 2.7k y 4.8k /año; influenciada por el contenido de nutrientes del suelo, la actividad microbiana y las condiciones climáticas (Quinto y Ramos 2009). Por su parte, se ha cuantificado una producción de hojarasca de 7.6 ton/ha/año; determinada por factores como la precipitación, y contenido de nutrientes del suelo (Quinto et al., 2007). Todo ello, muestra la complejidad del funcionamiento del bosque. No obstante, a pesar de su importancia, se desconoce qué efectos podría tener la minería sobre procesos como la PPN y reciclaje de nutrientes.

En consecuencia, la evaluación de la influencia de la minería sobre la PPN y el reciclaje de nutrientes de los bosques del Pacífico colombiano es crucial para entender los mecanismos de recuperación de estos ecosistemas. Debido a ello, nos planteamos el objetivo de determinar la influencia de la minería a cielo abierto y factores ambientales del ecosistema sobre la biomasa, PPN, y reciclaje de nutrientes en bosques tropicales del Chocó biogeográfico.

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Hipótesis de investigación.

Hipótesis alternativa 1:

La biomasa aérea de los árboles en bosques primarios y post-minería está influenciada por factores ecológicos y edáficos, como la estructura del bosque, la riqueza de especies y el contenido de nutrientes del suelo. Se espera que la biomasa aérea en bosques secundarios post-minería sea significativamente menor que en bosques primarios, pero que aumente con el tiempo de sucesión. La biomasa aérea de un bosque post-minería alcanzará la de un bosque primario después de varias décadas de sucesión, dependiendo de la tasa de acumulación de carbono en el ecosistema degradado por la minería.

Hipótesis alternativa 2:

La productividad primaria neta (NPP) de los bosques tropicales post-minería está influenciada por la fertilidad del suelo, especialmente por las limitaciones de nitrógeno (N) y fósforo (P). Se espera que la recuperación de la NPP en bosques degradados por minería sea lenta en los primeros años y que los nutrientes del suelo determinen la NPP, observándose una limitación múltiple de nutrientes con la sucesión. La restauración del ecosistema degradado es necesaria para mejorar la productividad y contribuir a la mitigación del cambio climático global.

Hipótesis alternativa 3:

La minería afecta el ciclo de nutrientes en los bosques tropicales, y se espera que el reciclaje de nutrientes sea menor en áreas post-minería en comparación con los bosques maduros. La minería influye de manera diferente en los contenidos de nutrientes del suelo, aumentando algunos nutrientes disponibles en áreas post-minería. La producción de hojarasca y la acumulación de masa de hojarasca en el suelo son mayores en áreas post-minería, mientras que la dinámica de la hojarasca es mayor en bosques maduros. Se observa una mayor eficiencia en el uso de nutrientes (NUE) en áreas post-minería como una estrategia para la conservación de nutrientes y la recuperación de la funcionalidad del ecosistema.

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Preguntas de investigación

1. ¿Cómo los factores ecológicos (diversidad, estructura, abundancia, riqueza de especies) y edáficos (acidez, textura y contenido nutrientes) afectan la biomasa aérea de los árboles en bosques tropicales maduros y de post-minería del Chocó biogeográfico? ¿Será que la influencia de los factores ecológicos y edáficos sobre la biomasa aérea de los árboles cambia debido a los efectos de la minería a cielo abierto en el Chocó biogeográfico?

2. ¿Cómo la fertilidad del suelo influye sobre la productividad primaria neta en bosques tropicales post-minería del Chocó biogeográfico? ¿En qué medida está influenciada la productividad primaria neta por los contenidos edáficos de Nitrógeno y Fósforo en bosques post-minería del Chocó biogeográfico?

3. ¿En qué medida la minería a cielo abierto puede afectar el reciclaje de nutrientes en bosques pluviales tropicales del Chocó biogeográfico? ¿Qué efectos tiene la minería a cielo abierto sobre la producción y descomposición de hojarasca en bosques pluviales tropicales del Chocó biogeográfico? ¿Qué efectos tiene la minería a cielo abierto sobre el contenido edáfico de nutrientes en bosques pluviales tropicales? ¿Qué efectos tiene la minería a cielo abierto sobre el contenido foliar de nutrientes y la eficiencia del uso de nutrientes en bosques pluviales tropicales del Chocó biogeográfico?

Objetivos

Objetivo general

Determinar la influencia de la minería a cielo abierto y factores ambientales (suelos y estructura del bosque) del ecosistema sobre la biomasa aérea arbórea, productividad primaria neta, y reciclaje de nutrientes en bosques lluviosos tropicales maduros y de post-minería del Chocó biogeográfico.

Objetivos específicos

1. Evaluar la influencia de los factores ecológicos (diversidad, estructura, abundancia, riqueza de especies) y edáficos (acidez, textura y contenido nutrientes) sobre la biomasa aérea de los árboles en bosques tropicales maduros y de post-minería del Chocó biogeográfico.

2. Evaluar la influencia de la fertilidad del suelo sobre la productividad primaria neta en bosques pluviales tropicales post-minería del Chocó biogeográfico.

3. Determinar los efectos de la minería a cielo abierto sobre la producción de hojarasca, contenido foliar y reciclaje de nutrientes del suelo en bosques pluviales tropicales del Chocó biogeográfico.

Metodología

1.Área de estudio

El estudio se llevó a cabo entre 2019 y 2022 en áreas boscosas previamente degradadas por la minería de oro a cielo abierto en el municipio de Jigualito (5º06'01" N - 76°32'44" O) y los bosques lluviosos y pluviales tropicales maduros de Opogodó (municipio de Condoto) en el departamento del Chocó, Colombia. Estos bosques, tanto maduros como post-mineros, están ubicados a menos de cinco kilómetros de distancia y presentan niveles similares de precipitación (media de 8000 mm anuales), altitud (70 m), temperatura (media de 26 ℃) y una topografía plana. La región forma parte de la biogeografía del Chocó Centro Norte, con suelos aluviales y un tipo de roca sedimentaria transicional (Poveda et al., 2004).

2. Diseño experimental

Se utilizó un diseño experimental estratificado por edad de sucesión, con dos estratos de muestreo. El estrato 1 abarcó áreas con 30-35 años de recuperación post-minería, caracterizadas por vegetación arbórea con mayor diámetro y riqueza de especies. El estrato 2 incluyó bosques primarios de la región, utilizados como referencia. En los bosques maduros, se establecieron 37 parcelas permanentes 10 × 10 m (100 m²), mientras que en los bosques post-minería se establecieron 125 parcelas permanentes de igual tamaño.

3. Medición de parámetros físicos y químicos del suelo

En cada parcela, se tomaron muestras compuestas de suelo a una profundidad de 20 cm para medir parámetros como acidez (pH), Al, MO, N total, P disponible, Ca, K, Mg, ECEC y textura (porcentajes de arena, limo y arcilla). Las muestras se analizaron siguiendo técnicas de laboratorio: fracciones texturales mediante Bouyoucos, pH en solución acuosa (1:2), MO con el método Walkley y Black, N total mediante Micro-Kjeldahl, P disponible con extracción Bray II y espectrofotometría UV-VIS, y absorción atómica para Ca, Mg y K (Quinto et al., 2022). Las muestras de suelos fueron enviadas al Laboratorio de Biogeoquímica de la Universidad Nacional de Colombia sede Medellín.

4. Medición de la producción de hojarasca

Se determinó la producción de hojarasca utilizando recolectores de hojarasca de 1.0 m × 0.5 m en un total de 75 recolectores en bosques maduros y 60 en post-minería. Los recolectores se distribuyeron de acuerdo con los tratamientos establecidos. El material recolectado se secó y pesó, y las cantidades se expresaron en toneladas por hectárea por año (t ha^{-1} $año^{-1}$) (Montagnini y Jordan, 2005).

Establecimiento de parcelas:

Dado que el objetivo de este estudio fue la evaluación de la biomasa aérea arbórea en función de factores ambientales y biológicos como tipo de bosque, tiempo de sucesión, abundancia de individuos, riqueza de especies, diámetro promedio, textura y nutrientes del suelo en distintos bosques y áreas degradadas por minería en el Chocó biogeográfico, se establecieron cinco parcelas permanentes de una hectárea, divididas en 25 cuadrantes de 20 x 20 m (400 m^2). Mientras que, en áreas degradadas por minería a cielo abierto de oro y platino en Jigualito, se establecieron cinco parcelas de 25 x 25 m (625 m^2), las cuales se subdividieron en 25 cuadrantes de 5 x 5 m (25 m^2) en un ecosistema con antecedente de actividad minera de más de 15 años de abandono. De forma similar, en otra área boscosa que previamente fue degradada por minería, pero con más de 30 años de regeneración, se instalaron cinco parcelas permanentes de 50 x 50 m (2.500 m^2); luego, al interior de cada unidad de muestreo se establecieron 25 cuadrantes de 10 x 10 m (100 m^2). Cada uno de los cuadrantes de las parcelas fueron empleados como unidades de muestreo (**Figura 1**), por lo que en ellos se realizaron las mediciones de suelos, diversidad, estructura y biomasa aérea de los árboles. Para los análisis y comparaciones entre unidades de muestreo, las variables fueron evaluadas a nivel de unidades de cuadrantes y de hectárea.

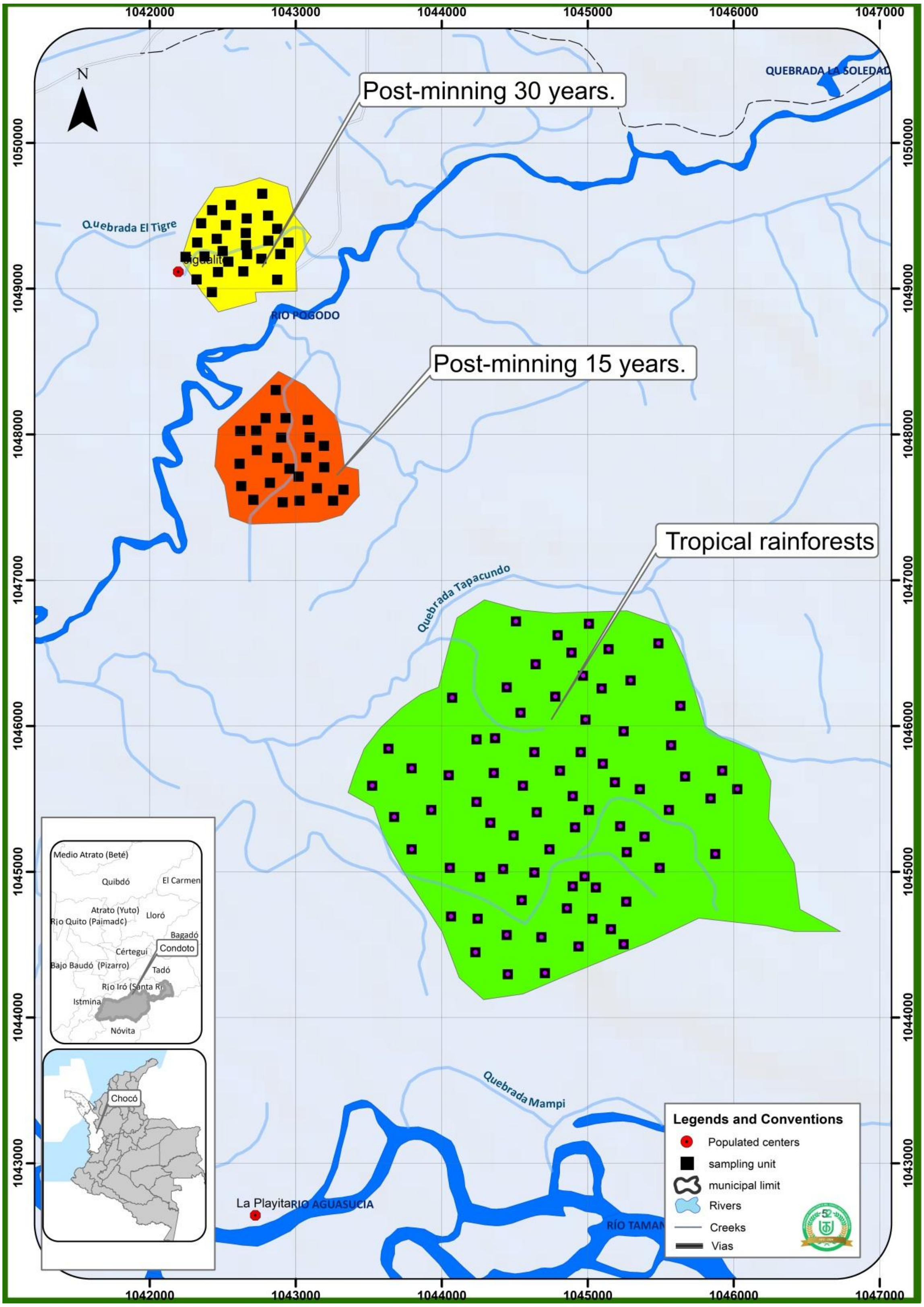

Figura 1 Mapa de Distribución de parcelas permanentes

Medición de diámetros y altura de los árboles.

En las parcelas establecidas se midió el diámetro a la altura del pecho (DAP) (1.30 m sobre el nivel del suelo) a todos los árboles con DAP ≥ 10 cm. Estas mediciones se realizaron en la parte cilíndrica del árbol, en áreas libres de nudos, ramas, bambas y/o raíces adventicias. Estas mediciones se realizaron entre los meses de agosto y octubre del año 2020 en los bosques de Jigualito. A los árboles medidos se les determinó el hábito de crecimiento en las categorías de árbol, bejuco o liana y palma, se anotaron las características y observaciones particulares de cada individuo. El perímetro del tronco del árbol donde se midió el diámetro (DAP) se marcó con pintura asfáltica amarilla para garantizar que todas mediciones se realizaran en la misma zona de la primera medición; además, se colocaron placas de aluminio para su posterior ubicación en la cuadrícula y parcela. La altura de los árboles se determinó con un Clinómetro Sutton a distancias fijas de 10 metros de los individuos. A los datos de diámetro y altura de los árboles se les determinó el promedio a nivel de unidades de muestreo o cuadrantes.

Identificación taxonómica y clasificación en grupos funcionales.

Se identificaron todas las morfoespecies hasta el máximo nivel taxonómico posible (indeterminados-NN, especie, género, familia botánica). Esta identificación se llevó a cabo utilizando claves especializadas y por confrontación con el material depositado en la colección del herbario CHOCO de la Universidad Tecnológica del Chocó. Con los datos taxonómicos de las parcelas permanentes se determinó la riqueza de especies, abundancia de individuos, dominancia de Simpson, equidad de Shannon, diversidad de Margalef, y dominancia de Berger-Parker (Quinto et al. 2019). Estos cálculos de diversidad se realizaron a nivel de unidades de muestreo o cuadrantes, para comparar en la misma escala con las demás variables ambientales y biológicas.

Estimación y clasificación de la densidad de la madera.

Para estimar esta variable se tomaron los valores publicados en dos bases de datos internacionales de densidad de madera generadas en bosques tropicales (Baker et al. 2004); en los casos en los que alguna especie o género encontrado en las parcelas no se estuviese reportado en estas bases de datos, se empleó el promedio del género o de la familia, para los individuos indeterminados taxonómicamente se empleó el promedio de la parcela.

Estimación de la biomasa aérea del bosque.

para la determinación de la biomasa aérea de los árboles se emplearon ecuaciones alométricas diseñadas para bosques muy húmedos y pluviales tropicales. La ecuación empleada fue la propuesta por Álvarez et al. (2012):

$$BA = \exp(-2{,}857 + 2{,}081 \cdot \ln DAP + 0{,}587 \cdot \ln Al + 0{,}453 \cdot \ln Dm)$$

Donde el BA es la biomasa aérea de los árboles en kilogramos, DAP es el diámetro a la altura del pecho de los árboles, Al es la altura total de los árboles, Dm es la densidad de la madera, y ln es el logaritmo neperiano.

Medición de la descomposición de la hojarasca.

La descomposición se midió mediante el método de bolsas de descomposición. Se recolectaron hojas recientemente caídas de especies arbóreas dominantes, que se secaron hasta alcanzar un peso seco constante. Se introdujeron 100 g de hojarasca seca en cada bolsa y se colocaron en los bosques. Semanalmente durante 32 días, se recolectaron 10 bolsas aleatorias para determinar la cantidad de peso seco perdido y calcular la tasa de descomposición (*k*) mediante el modelo exponencial simple (Vitousek y Sanford, 1986). Para calcular matemáticamente la descomposición de hojarasca se empleó el modelo exponencial simple (K) propuesto por Olson (1963):

$$Ln(X0/X1) = K*T$$

$$K = Ln(X0/X1)/T$$

Donde X0 es la masa inicial, X1 es la masa final remanente en el tiempo T; y T es el tiempo transcurrido en años.

Medición del contenido de nutrientes de las hojas.

En cada parcela, se tomaron muestras compuestas de hojarasca seca, a las cuales se les midieron parámetros como N, P, Ca, K y Mg. Las técnicas de laboratorio incluyeron Micro-Kjeldahl para N total, espectrofotometría UV-VIS para P disponible, y absorción atómica para Ca, Mg y K (Osorio, 2021).

Análisis de datos.

Para evaluar la influencia de la minería sobre los PPN, biomasa aérea, y reciclaje de nutrientes, se utilizó la prueba no paramétrica de Mann-Whitney (MW) cuando no se cumplieron los supuestos de normalidad y homogeneidad de varianzas. En caso contrario, se utilizó la prueba T-Student. Los análisis estadísticos se realizaron en Rstudio versión 3.0.0.

Para evaluar el efecto de los factores: tipo de bosque, tiempo de sucesión, abundancia de individuos, diámetro promedio, altura promedio, riqueza de especies, equidad de Shannon, diversidad de Margalef, dominancia de Berger-Parker, acidez, porcentaje de materia orgánica y nitrógeno total, contenidos de fósforo, aluminio, calcio, magnesio y potasio, capacidad de intercambio catiónico efectiva – CICE, porcentajes de arena, arcilla y limo, sobre la biomasa aérea de los árboles se evaluaron inicialmente la normalidad de los datos con los estadísticos de Bartlett, Hartley y Kurtosis. Luego, para evaluar la variación de la biomasa aérea de árboles en función del tipo de bosque (bosque primario y bosque en recuperación de la minería), tiempo de sucesión (15, 30 y 300 años) y entre las localidades (Jigualito, Opogodó y Pacurita) se utilizaron pruebas no paramétricas de Mann-Whitney, Kruskal-Wallis (Kw) y la prueba de rangos múltiples de Duncan; dado que los datos no cumplieron los supuestos (normalidad y homogeneidad de varianzas) para pruebas paramétricas.

Para determinar la influencia de variables como: tipo de ecosistema, abundancia de individuos, diámetro promedio, altura promedio, riqueza de especies, dominancia de Simpson, equidad de Shannon, diversidad de Margalef, dominancia de Berger-Parker, acidez, porcentaje de materia orgánica y nitrógeno total, contenidos de fósforo, aluminio, calcio, magnesio y potasio, capacidad de intercambio catiónico efectiva – CICE, porcentajes de arena, arcilla y limo, en conjunto sobre la biomasa aérea de los árboles se emplearon Modelos Lineales Generales (MLG), y una Regresión Múltiple con una selección de variables significativas con el método "hacia atrás" (backward). Este análisis se realizó a nivel general (con todos los ecosistemas), en los bosques primarios y en las áreas boscosas previamente degradadas por minería. Los análisis se realizaron a nivel de unidades de muestreo (cuadrantes). Los análisis de diversidad (dominancia de Simpson, equidad de Shannon, de Margalef, y dominancia de Berger-Parker), las pruebas de Mann-Whitney, Kruskal-Wallis, Duncan, MLG, y regresión múltiple se realizaron en el entorno de programación R (R Core Team 2012).

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Resultados

Artículo 1: Biomasa Aérea y Factores Ambientales

El primer estudio examinó cómo las variables estructurales —como el diámetro a la altura del pecho (DAP), la altura total y la densidad de la madera— junto con características edáficas, influyen en la acumulación de biomasa aérea en bosques tropicales. Los análisis realizados revelaron que la biomasa se incrementa de forma exponencial en función del DAP y la altura, evidenciándose una relación altamente significativa ($p < 0.001$) con un coeficiente de determinación (R^2) cercano a 0.80 (Pérez et al., 2025). Además, se observó que la biomasa aérea en áreas afectadas por la minería es considerablemente menor en comparación con la de los bosques primarios. Esta diferencia se atribuye a la alteración de la estructura forestal, la pérdida de especies y al deterioro de las propiedades del suelo inducido por la actividad minera. Los datos se presentan a través de tablas resumen y gráficos de dispersión que ilustran, por un lado, la relación entre el DAP y la biomasa, y por otro, la distribución comparativa de la biomasa en bosques primarios y áreas post-minería.

How to cite: Abadía, D.P. Quinto-Mosquera, H.Q. Del Arco, J.M. (2025). Influence of Environmental Factors on the Aboveground Biomass of Mature and Postmining Forests in Chocó. ***Life*** 2025, 15, 98.
https://doi.org/10.3390/life15010098

Academic Editor: Naiqing Pan Received: 21 November 2024
Revised: 7 January 2025
Accepted: 8 January 2025
Published: 15 January 2025

Artículo 2: Ciclaje de Nutrientes en Bosques Afectados por la Minería

El segundo estudio se centró en evaluar el efecto de la minería a cielo abierto sobre el ciclo de nutrientes en bosques tropicales. Los resultados indicaron que, en suelos post-minería, se registra un incremento significativo en la disponibilidad de nutrientes esenciales, como el fósforo (P), el potasio (K), el calcio (Ca) y el magnesio (Mg). Sin embargo, se detectaron también concentraciones elevadas de aluminio (Al), lo que podría generar efectos tóxicos y limitar el crecimiento de la vegetación (Quinto-Mosquera et al., 2024a). Adicionalmente, se constató que la producción de hojarasca en las áreas degradadas por minería es mayor que en los bosques primarios, mientras que la tasa de descomposición de la hojarasca es significativamente inferior. Estos hallazgos sugieren la existencia de un mecanismo de conservación de nutrientes en los ecosistemas perturbados, en el que la acumulación de materia orgánica podría favorecer la regeneración a largo plazo. Los resultados se apoyan en análisis comparativos presentados en tablas y en diagramas de barras que evidencian las diferencias estadísticamente significativas entre los distintos tipos de bosque.

How to cite: Mosquera HQ, Cuesta HV, Abadía DP. Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian
Pacific. Rev Bras Cienc Solo.2024;48:e0230053
https://doi.org/10.36783/18069657rbcs20230053

Editors: José Miguel Reichert and Jeferson Dieckow .

Received: May 23, 2023
Approved: October 17, 2023

Artículo 3: Productividad Primaria Neta y Fertilidad del Suelo

El tercer estudio investigó la relación entre la fertilidad edáfica y la productividad primaria neta (PPN) en bosques post-minería. Los análisis de correlación y regresión múltiple demostraron que la PPN está fuertemente condicionada por la disponibilidad de nutrientes, especialmente por el nitrógeno (N) y el fósforo (P). Se observó una correlación positiva significativa entre el contenido de fósforo y la PPN ($r \approx 0.65$, $p < 0.01$), lo que subraya la importancia de este nutriente en la recuperación del ecosistema (Quinto-Mosquera et al., 2024b). Asimismo, las áreas post-minería presentan valores de PPN inferiores a los de los bosques primarios; no obstante, se evidencia una tendencia a la mejora de la productividad a medida que aumenta el tiempo de regeneración y se restablecen las condiciones edáficas favorables. Estos resultados se ilustran mediante gráficos de dispersión que muestran la relación entre el contenido de fósforo y la PPN, y mediante tablas que resumen los coeficientes de regresión y la significancia estadística de las variables analizadas.

Citation: Quinto Mosquera, H[1].; Torres-Torres, J.J[2].; Pérez-Abadía, D. (2024)[3]. Influence of Mining on Nutrient Cycling in the Tropical Rain Forests of the Colombian Pacific. ***Forests*** 2024, 15, 1222. https://doi.org/10.3390/f15071222

Academic Editors: Songze Wan, Jianping Wu and Shaofei Jin

Received: 23 June 2024

Revised: 12 July 2024

[1] Harley Quinto Mosquera: Biology Program, School of Natural Sciences, Universidad Tecnológica del Chocó Diego Luis Córdoba, Quibdó, Chocó 270002, Colombia

[2] Jhon Jerley Torres-Torres: Agroforestry Engineering Program, Faculty of Engineering, Universidad Tecnológica del Chocó Diego
Luis Córdoba, Quibdó, Chocó 270002, Colombia; i-jhon.torres@utch.edu.co

[3] University Institute for Research in Sustainable Forest Management, Universidad de Valladolid, 47002 Palencia, Spain; davidfernandoperez@gmail.com

*Correspondence: d-harley.quinto@utch.edu.co; Tel.: +57-3218154729

Accepted: 12 July 2024

Published: 14 July 2024

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Artículo 1

Influence of Environmental Factors on the Aboveground Biomass of Mature and Postmining Forests in Chocó

David Pérez Abadía [4,5], Harley Quinto Mosquera[6] and José María Del Arco[7]

Abstract

Environmental factors control the accumulation of aboveground biomass (AB) in tropical forests, along with the role of AB in climate change mitigation. As such, the objective of this study was to evaluate the influence of factors such as forest type, succession, abundance of individuals, species richness, height, diameter, texture, and soil nutrient levels on the AB in mature and postmining forests in Chocó, Colombia. Five plots each were set up in primary and postmining forests with 15 and 30 years of regeneration, in which the amount of AB was measured and related to the environmental factors. The AB was 178.32 t ha^{-1} in the mature forests and 35.17 and 56.3 t ha^{-1} after 15 and 30 years of postmining regeneration, respectively. Furthermore, the general AB level was determined by the ecosystem type, diameter, richness, abundance, Shannon evenness, and Margalef di- versity. In mature forests, the AB amount was positively influenced by height and richness, and negatively influenced by dominance and evenness; in areas degraded by mining, the AB level was positively related to richness and equity, and negatively related to species diversity and soil silt. In summary, environmental factors determine the

[4] Doctorate Program in Conservation and Sustainable Use of Forest Systems, University Institute for Research in Sustainable Forest Management, University of Valladolid, 34004 Palencia, Spain; davidfernandoperez@gmail.com

[5] Agroforestry Engineering Program, Faculty of Engineering, Technological University of Chocó Diego Luis Córdoba, Quibdó 270001, Colombia

[6] Biology Program, Faculty of Natural Sciences, Technological University of Chocó Diego Luis Córdoba, Quibdó 270001, Colombia

[7] Department of Agroforestry Sciences, Institute of Sustainable Forest Management Research UVa_INIA, E.T.S. (Higher Technical School) of Agrarian Engineering of Palencia, University of Valladolid, 34004 Palencia, Spain; josemaria.arco@uva.es*

Correspondence:d-harley.quinto@utch.edu.co

carbon storage in the forests in Chocó. Mining reduces the function of these ecosystems in mitigating climate change.

Keywords: biodiversity; carbon; global climate change; secondary forests; succession.

Introduction

Tropical forests are considered the most important terrestrial ecosystems on the planet due to their geographical extent, ecological complexity, high biodiversity, and rates of endemism [1,2]. In addition, tropical forests play a fundamental role in the global carbon balance and the mitigation of global warming, due to their high rates of atmospheric carbon capture and storage [2,3]. Pan et al. [2] reported that primary forests have the highest tree biomass (aboveground + belowground), with an average of 327.8 tons per hectare (t ha^{-1}) [2]. Additionally, the aboveground biomass (AB) amount in tropical rainforests was found to be between 174.23 and 541.6 t ha^{-1} [4]. Thus, the relevance of these terrestrial ecosystems in terms of mitigating global climate change has been verified [3]; however, the amount of AB in different tropical regions varies widely

The large variation in the AB recorded in tropical forests is largely due to its complexity and ability to be influenced by climatic (precipitation, temperature, and humidity), biologi- cal (species composition, type of species, and ecological group), and environmental (age of the substrate, soil fertility, topography, and altitude) factors. Furthermore, the accumula- tion of AB involves processes such as plant establishment, growth, mortality, succession, and disturbances [5–7]. Asner et al. [5] observed that the amount of AB is determined by soil drainage, precipitation, temperature (altitude), dominant species composition, and substrate age in tropical rainforests in Hawaii [5]. Oberleitner et al. [8] reported that the amount of AB is related to the age of the substrate, forest cover, and species richness in forests in Costa Rica. These studies demonstrate the importance of environmental and biological factors in the accumulation of AB in tropical forests.

Poorter et al. [6] found that the AB of trees is strongly affected by precipitation, average tree diameter, and species diversity through an analysis at the neotropical forest scale; soil fertility was weakly related to biomass [6]. For this reason, and based on the results of Asner et al. [5], Poorter et al. [6], and Oberleitner et al. [8], we expected the highest amounts of AB and carbon accumulation to be found in tropical forests with high levels of rainfall and species diversity. However, we need to understand the processes that occur in tropical forests with high rainfall in the relationship between these environmental factors and AB accumulation. To answer this question, we evaluated the AB accumulation in forests with high rainfall and biodiversity. Although Poorter et al. [6] studied 59 sites and 2050 permanent research plots, the range of precipitation in the area was between 750 and 4350 mm annually. Therefore, how environmental and biological factors influence the AB in tropical forests with higher rainfall is unknown. The biogeographical region of Chocó provides a suitable context in which to study the influence of these factors on AB under excessive rainfall conditions. Chocó is characterized by high biodiversity, lowland forest ecosystems, and one of the highest rainfall totals in the world (≈10,000 mm annually) [1,9], providing a suitable site to study the relationship between environmental factors and AB accumulation under high rainfall amounts.

In the forests of Chocó, the stocks and flows of biomass and carbon have been quan- tified. Faber-Langendoen and Gentry [10] estimated the AB in the forest ecosystems of Tutunendo and Bajo Calima as being between 178.1 and 210.9 t ha^{-1} on acidic soils that were poor in nutrients and rich in organic matter [10]. Three decades later, AB values of between 156.8 and 217.85 t ha^{-1} were recorded in the tropical rainforests in the towns of Opogodó and Pacurita in the region, with AB accumulation rates of 7.8 and 10.9 t ha^{-1} $year^{-1}$, re- spectively [11]. However, the influence of species richness, forest type, soil nutrients, and variation in precipitation on the AB in the region (which has one of the highest annual rainfall amounts in the world) was unknown.

The Chocó forests, with their high biodiversity and endemism [1], play an important role in mitigating global climate change, having a forest area of ≈7.8 million hectares in Colombia, of which 80% are well-preserved and mature forests.

However, those in the local communities constantly carry out open-pit mining for gold and platinum in these ecosystems, which destroys and degrades approximately 360 hectares of forest each year [12]. These activities considerably reduce the AB in these ecosystems and the ability of these ecosystems to contribute to the mitigation of global climate change because, after mining, the ecosystem requires more than 300 years to recover [13]. As such, in this study, we aimed to answer the following question: how do environmental and biological factors such as forest type (primary and secondary), succession time, abundance, tree species dominance, species richness, diameter, texture, and soil drainage affect the variation in AB amount in mature and postmining forests in Chocó, an area with one of the highest rainfall amounts in the world?

Materials and Methods

Study Area

This study was conducted in different forests of Chocó, Colombia, specifically in the trop- ical rainforests of the towns of Pacurita (5°41′55″ N, 76°35′59″ W) and Opogodó (5°04′07″N, 76°64′74″W), as well as in the secondary forests of Jigualito (5°06′01″ N, 76°32′44″ W) (Figure 1). These forests were in different stages of succession due to open-pit mining activity. These areas are part of the north central subregion of Chocó, which includes the upper basins of the Atrato and San Juan Rivers and features foothill and low hill landscapes, humid terrace soils, and transitional sedimentary rock [9]. The annual rainfall and altitude of the Opogodó forests are 8000 mm and 80 m, respectively, and the topography is mostly flat. The annual precipitation and altitude in Pacurita are 10,000 mm and 130 m, respectively, and the topography is broken [11]. In Jigualito, the annual precipitation is 8000 mm, the altitude is 70 m and the topography flat. The forests in this locality are mostly secondary, determined by the time when open-pit mining activities were halted. Consequently, the forests are in various stages of recovery after open-pit gold and platinum mining activities were conducted at different times, which have led to the formation of forests in different successional stages [13]. A map of the study area is provided.

The soils of the four forests studied were Ultisols that differed in their nutrient contents and texture. Specifically, the soils were extremely acidic, with high aluminum saturation in the Salero and Pacurita forests. The soils of the Opogodó forests had high concentrations of OM and total N. The edaphic P, Mg, Ca, and CICE values were low, those of K were intermediate [11]. The soils of Jigualito, an area in which mining activities were previously carried out, were characterized by large amounts of rocky material and sand. The soils in this area were acidic, with high contents of OM, P, and total N, as well as intermediate concentrations of Mg and K. However, the calcium content was low, and the aluminum content was high (Table 1).

Tabla 1 Structural, ecological, and edaphic characteristics of the primary and recovering (from abandoned mines) fotests evaluated in Chocó

Location	Pacurita	Opogodó	Jigualito	
Ecosystem Type	Primary Forests		Abandoned Mine	
Succession Time (Years)	≈300		15	30
Average tree diameter in quadrat	15.99	16.86	5.57	13.89
Average tree height in quadrat	15.44	15.83	7.46	13.44
Richness	22.96	19.11	5.56	8.68
Abundance	37.82	30.64	11.12	17.36
Simpson diversity	0.06	0.08	0.31	0.31
Shannon	2.97	2.77	1.42	1.44
Margalef	6.07	5.31	1.75	1.73
Berger–Parker index	0.13	0.15	0.44	0.43
pH	4.03	4.98	4.64	4.47
Organic matter (%)	4.07	11.94	5.07	10.26
Phosphorus (ppm)	1.37	1.33	30.73	26.16
Total nitrogen (%)	0.20	0.61	0.23	0.40
Aluminum (cmol/kg)	0.94	0.13	2.84	3.29
Calcium (cmol/kg)	0.35	0.39	1.28	2.85
Magnesium (cmol/kg)	0.18	0.28	1.35	1.60
Potassium (cmol/kg)	0.17	0.23	0.51	0.34
ECEC (cmol/kg)	1.65	1.03	5.71	8.40
Sand (%)	53.36	85.72	66.08	73.41
Silt (%)	28.12	13.24	23.84	20.35
Clay (%)	18.52	1.04	10.08	6.06

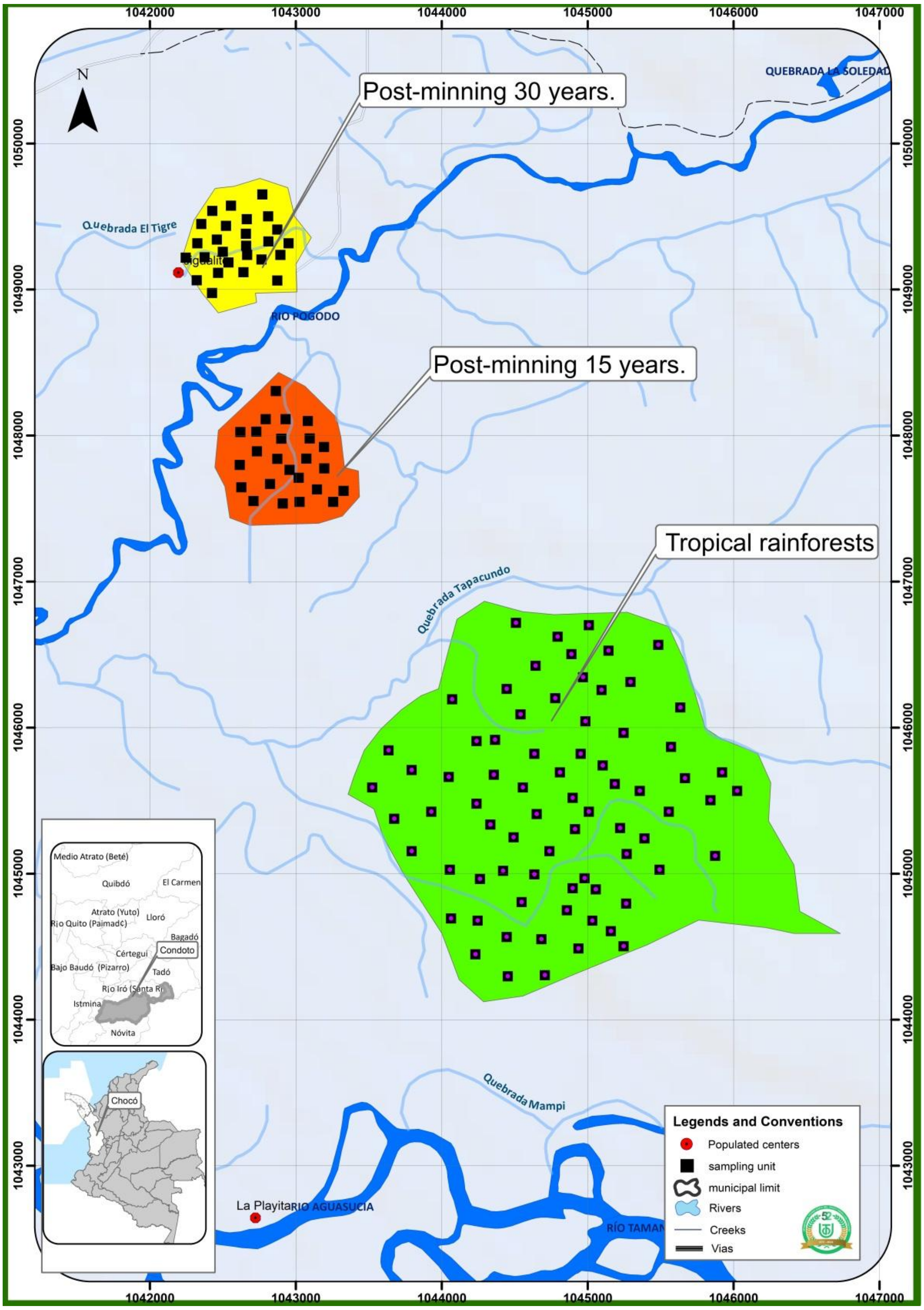
Post-minning 30 years.
Post-minning 15 years.
Tropical rainforests
Quebrada El Tigre
RÍO POGODO
QUEBRADA LA SOLEDAD
Quebrada Tapacundo
Quebrada Mampi
La Playita
RÍO AGUASUCIA
N
Legends and Conventions
Populated centers
sampling unit
municipal limit
Rivers
Creeks
Vias
Medio Atrato (Beté)
Quibdó
El Carmen
Atrato (Yuto)
Río Quito (Paimadó)
Lloró
Bagadó
Cértegui
Condoto
Bajo Baudó (Pizarro)
Tadó
Istmina
Nóvita
Chocó
1042000
1043000
1044000
1045000
1046000
1047000
1050000
1049000
1048000

FIgura 2 Study area, Chocó, Colombia

The composition of the tree layer in Opogodó was dominated by species such as Wettinia quinaria, Mabea occidentalis, Calophyllum auratum, Eschweilera sclerophylla, and Oenocarpus bataua. The Pacurita tree layer was dominated by Calophyllum aura- tum, Eschweilera sclerophylla, Oenocarpus bataua, Protium apiculatum, and Brosimum utile. Opogodó was dominated by botanical families such as the Arecaceae, Fabaceae, Lecythidaceae, Hypericaceae, Sapotaceae, and Euphorbiaceae. The dominant families in Pacurita were the Arecaceae, Sapotaceae, Lecythidaceae, Clusiaceae, Moraceae, and Chrysobalanaceae [14]. Between 75 and 90 tree species per hectare have been recorded in the forests of Opogodó; an average of 95 species per hectare has been recorded in Pacurita.

The dominant species in the forests of Jigualito were Anthurium formosum, Anthurium alatum, Philodendron acutatum, Cespedesia spathulata, Croton chocoanus, Glossoloma, and Tonina fluviatilis, with botanical families such as the Annonaceae, Areaceae, Asteraceae Buseraceae, Chrysobalanaceae, Clusiaceae, Cyatheaceae, and Melastomataceae. Table 1 summarizes the structural, ecological, and edaphic characteristics of the primary and recovering forests (abandoned mines) evaluated in this study.

Plot Establishment

Five permanent 1 ha plots were established, divided into 25 quadrats measuring 20 × 20 m (400 m^2), which we used as the sampling units in the primary forests of Opogodó and Pacurita. Five plots measuring 25 × 25 m (625 m^2) were established in the areas degraded by open-pit gold and platinum mines in Jigualito that had been abandoned for more than 15 years, which were subdivided into 25 quadrats measuring 5 × 5 m (25 m^2). Similarly, five permanent plots measuring 50 × 50 m (2500 m^2) were installed in another forest area that was degraded by mines, which had been regenerating for more than 30 years. Within each sampling unit, 25 quadrats measuring 10 × 10 m (100 m^2) were established. Each of the quadrats in the plots was used as a sampling unit for measurements of soil, diversity, structure, and AB of the trees. For comparisons between sampling units, the variables were evaluated at the quadrat and hectare levels.

Measurement of Tree Diameter and Height

The diameter at breast height (DBH) (1.30 m above ground level) was measured for all trees with DBH ≥ 10 cm in the established plots. These measurements were recorded from the cylindrical part of the tree in areas free of nodes, branches, buds, and/or adventitious roots between the months of August and October 2020 in the Jigualito, Opogodó, and Pacurita forests. The growth habit of the measured trees was categorized as tree, vine, liana, and palm; the particular characteristics and observations of each individual were noted. The perimeter of the tree trunk where the DBH was measured was marked with yellow asphalt paint to guarantee that all subsequent measurements were recorded in the same area as the first measurement. In addition, aluminum plates were placed on the grid and plot. The tree height was determined with a Sutton Clinometer at fixed distances of 10 m from the individuals. The diameter and height data of the trees were averaged at the sampling unit or quadrate level.

Taxonomic Identification and Classification into Functional Groups

All morphospecies were identified up to the highest possible taxonomic level (indeter- minate NN, species, genus, and family) using specialized keys and via comparison with the material deposited in the collection of the CHOCO herbarium of the Technological University of Chocó. Species richness and the abundance of individuals, as well as the Simpson, Shannon diversity, Margalef, and Berger–Parker indices were determined using the taxonomic data from the permanent plots [14]. These diversity indices were calcu- lated at the sampling unit or quadrat level for comparison on the same scale as the other environmental and biological variables.

Estimation and Classification of Wood Density

The values published in two international databases of wood density generated in tropical forests were used to estimate and classify wood density [15]. The average of the genus or family was used for cases where a species or genus in the plots was not reported in these databases. The average of the plot was used for taxonomically indeterminate individuals.

Soil Analysis

Composite soil samples were obtained at a depth of 20 cm with a cylindrical borehole in each of the sampling units (quadrats). The soil samples were sent to the Biogeochemistry Laboratory of the National University of Colombia, Medellín headquarters, where the physicochemical parameters of the soil were determined using the following techniques: texture with the Bouyoucos method; pH with a soil potentiometer; water/organic matter (OM) 1:2 with the Walkley and Black method and volumetrics; nitrogen with the Micro- Kjeldahl method; phosphorus with L ascorbic acid and UV–Vis spectrophotometry; and Ca, Mg, and K with 1 N ammonium acetate and the neutral and atomic absorption method [11].

Forest AB Estimation

Allometric equations designed for humid and tropical rain forests were used to de- termine the AB in the forests. The equation proposed by Álvarez et al. [16] was used because it was generated using data on the wood density, diameter, and height of trees in the Colombian Pacific region:

$$AB = \exp(-2.857 + 2.081 \times \ln DBH + 0.587 \times \ln TH + 0.453 \times \ln Dw)$$

where *AB* is the aboveground biomass of the trees in kilograms, *DBH* is the diameter at breast height of the trees, TH is the total height of the trees, *Dw* is the density of the wood, and ln is the natural logarithm.

General Data Analysis

Normality was initially evaluated with the Shapiro–Wilk and kurtosis tests to evaluate the effects of the following factors of AB: forest type; succession time; abundance of individuals; average tree diameter; average tree height, species richness; Shannon diversity, Margalef, and Berger–Parker indices; acidity; organic matter, total nitrogen, phosphorus, aluminum, calcium, magnesium, and potassium contents; effective cation exchange capac- ity (ECEC); and percentages of sand, clay, and silt. Then, nonparametric Mann–Whitney, Kruskal–Wallis (Kw), and Duncan's multiple range tests were used to evaluate the variation in the AB of the forests, depending on the type of forest (primary or postmining forest), succession duration (15, 30, or 300 years), and location, because the data did not meet the assumptions (normality and homogeneity of variances) for parametric tests. The tree height and diameter values were determined for each individual, whereas the variables used in the analyses of average DBH and average tree height were determined at the quadrat and plot levels in the estimation of BA.

Principal component analysis (PCA) and general linear models (GLMs) were used to determine the influence of the variables on the aboveground biomass of the trees. Multiple regression was performed with a selection of the significant variables using the backward method. This analysis was conducted at the general level (with all ecosystems) for the primary forests and successional forests (previously degraded by mining) and at the sampling unit (quadrat) level. Diversity analyses (Simpson, Shannon, Margalef, and Berger–Parker indices), as well as Mann–Whitney, Kruskal–Wallis, Duncan's, MLG, and multiple regression tests, were performed in the R programming environment [17].

Results

The AB of trees in the primary forests in Chocó presented an average (±standard error) value of 178.32 ± 13.2 t ha^{-1}, while, in the recovering forests that were previously affected by open-pit mining, the AB was 45.7 ± 3.5 t ha^{-1}, with statistically significant differences between these forest types (Mann–Whitney = 9.405; p-value < 0.0001). The average AB values were 35.17 ± 5.6

and 56.3 ± 3.05 t ha^{-1} in the forests after 15 and

30 years of succession after mining, respectively. The AB did not significantly differ among the areas previously degraded by mining, but the average AB significantly differed from that in the primary forests (Kruskal–Wallis = 90.25; p-value < 0.0001). Significant differences were noted in the AB between locations (Kruskal–Wallis = 94.38; p-value < 0.0001). We observed that the average AB was highest in the Pacurita forests, at 214.82 t ha^{-1}, and lowest in the recovering forests of Jigualito, at 45.73 t ha^{-1} (Table 2). In summary, the AB amount differed depending on the type of forest, succession duration, and locations.

Tabla 2 Aboveground biomass

*(t ha^{-1}) of trees according to forest type, succession duration (years), and location. The aboveground biomass values are reported as the average ± standard error; the letters a, b, and c indicate significant differences between the aboveground biomass averages. The asterisks (*) indicate the significance of the test: ***, p-value < 0.001; ND, not significant*

Aboveground Biomass		Mann–Whitney Test
Primary forests	178.32 ± 13.29 *a*	9.405 ***
Successional forests (mines)	45.73 ± 3.5 *b*	
Succession Duration (years)	**Aboveground Biomass**	**Kruskal–Wallis Test**
15 years (abandoned mines)	35.17 ± 5.6 *b*	90.25 ***
30 years (abandoned mines)	56.3 ± 3.05 *b*	
300 years (forest)	178.32 ± 13.29 *a*	
Location	**Aboveground Biomass**	**Kruskal–Wallis Test**
Pacurita (forest)	214.82 ± 26.98 *a*	94.38 ***
Opogodó (forest)	153.98 ± 12.33 *b*	
Jigualito (abandoned mines)	45.73 ± 3.5 *c*	

Regarding the environmental, structural, and ecological factors affecting the AB in all studied forests, AB was significantly determined by the type of ecosystem, average diameter, species richness, abundance of individuals, and the Shannon and Margalef in- dices (F test = 12.94; *p*-value < 0.001). In this analysis, the variables explained 38.1% of the variation in the AB (Table 3). In primary forests only (Pacurita and Opogodó), the AB was significantly positively influenced by the average tree height and species richness, and negatively influenced by dominance and Shannon's equity (F test = 24.45; *p*-value < 0.001). In this analysis, the variables explained 44.49% of the variation in the AB (Table 4). Finally, in areas previously degraded by mining, AB was significantly related to species richness and Shannon's diversity index, and negatively related to the Margalef index and the per- centage of soil silt (F test = 10.77; p-value < 0.001). In this analysis, the variables explained 54.2% of the variation in the AB (Table 5). The results of the general linear model (GLM) showed that the interaction of variables such as successional stage*nitrogen (F test = 4.27; p-value = 0.0411), successional stage*organic matter (F test = 5.97; p-value = 0.0161), suc- cessional stage*phosphorus (F test = 3.48; p-value = 0.064), successional stage*organic mat- ter*richness (F test = 4.65; p-value = 0.033), and successional stage*dominance (F test = 5.21; p-value = 0.024) significantly influenced aboveground biomass (Table S1 in the Supple- mentary Materials). The PCA results showed that the AB, Margalef index, Shannon index, species richness, basal area, abundance of individuals, tree height, and tree diameter, as well as nitrogen, organic matter, and sand contents were collinearly related (Figure 2). The PCA results showed that the Simpson and Berger–Parker indices, as well as phosphorus, potassium, aluminum, magnesium, calcium, and silt contents, were collinearly related, especially in forests degraded by mining (Figure 2). PC1 and PC2 explained 71.6% and 28.4% of the variation, respectively (Figure 2).

Table 3 Analysis of variance for aboveground biomass of trees as a function of structural and ecological variables for primary forests and abandoned mines of Chocó biogeographic region. Where R^2 *= 41.3%,* R^2 *(adjusted) = 38.1%.*

	Sum of Squares	Gf	Middle Square	F Test	*p*-Value
Model	1.40584×10^6	9	156,205	12.94	0.0000
Residue	1.9915×10^6	165	12,069.7		
Total (Corr.)	3.39735×10^6	174			
	Sum of Squares	**Gf**	**Middle Square**	**F Test**	***p*-Value**
Ecosystem type	37,957.9	1	37,957.9	3.14	0.0780
Average diameter	85,029.3	1	85,029.3	7.04	0.0087
Average height	2585.05	1	2585.05	0.21	0.6441
Richness	73,722.9	1	73,722.9	6.11	0.0145
Abundance	17,289.0	1	17,289.0	14.32	0.0002
Dominance Simpson	8010.23	1	8010.23	0.66	0.4164
Shannon	47,677.5	1	47,677.5	3.95	0.0485
Margalef	18,044.3	1	18,044.3	14.95	0.0002
Berger–Parker	427.072	1	427.072	0.04	0.8510
Residue	1.9915×10^6	165	12,069.7		
Total (Corr.)	3.39735×10^6	174			

Tabla 4 Analysis of variance and multiple regression for aboveground tree biomass as a function of structural and ecological variables for primary forests in Chocó.

R^2 = 46.39%, R^2 (adjusted) = 44.49%. The *backward* method was used to select significant variables.

	Sum of Squares	Gf	Middle Square	F Test	*p*-Value
Model	1.22119×10^6	4	30,529.8	24.45	0.0000
Residue	1.41114×10^6	113	12,487.9		
Total (Corr.)	2.63233×10^6	117			
Parameter	**Estimate**		**Standard Error**	**T Test**	***p*-Value**
Constant	3032.31		1022.98	2.9642	0.0037
Average tree height	59.1381		8.07487	7.32372	0.0000
Richness	71.6219		11.2447	6.36938	0.0000
Dominance	−7496.03		2399.16	−3.12444	0.0023
Shannon’s diversity	−1660.65		381.752	−4.35007	0.0000

Tabla 5 Results of analysis of variance and multiple regressions for aboveground tree biomass as a function of structural and ecological variables for forested abandoned mine areas in Chocó

R^2 = 59.75%, R^2 (adjusted) = 54.2%, and the *backward* method was used to select significant variables.

	Sum of Squares	Gf	Middle Square	F Test	*p*-Value
Model	15,812.3	4	3953.08	10.77	0.0000
Residue	10,648.2	29	367.18		
Total (Corr.)	26,460.5	33			
Parameter	**Estimate**		**Standard Error**	**T Test**	***p*-Value**
Constant	−35.3703		18.2267	−1.94058	0.0621
Richness	8.66422		2.02823	4.27182	0.0002
Shannon	79.2255		29.0122	2.73077	0.0106
Margalef	−57.0007		17.2118	−3.31172	0.0025
Silt	0.422064		0.20531	2.05574	0.0489

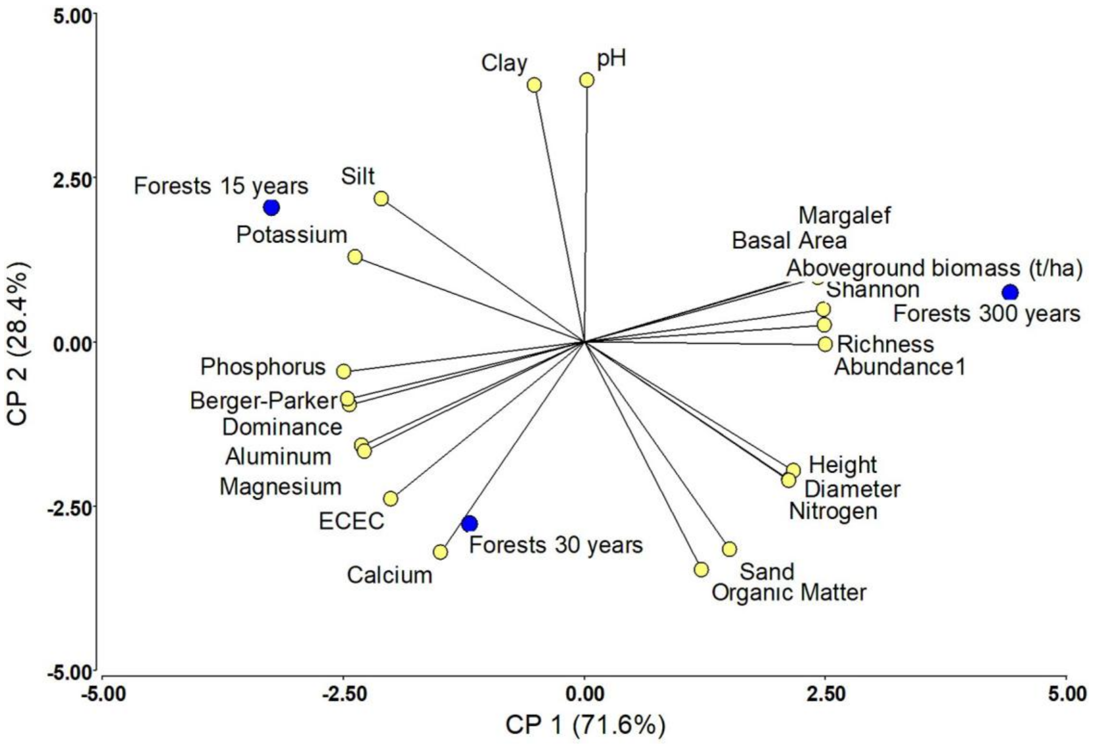

FIgura 3 Principal component analysis (PCA) of ecological variables

(biomass, structure, richness, and diversity) and edaphic variables (nutrients and texture) of primary and postmining forests in biogeographical region of Chocó.

Discussion

Aboveground Biomass of Trees in Primary Forests and Forests Degraded by Mining in Chocó

The aboveground biomass of the trees (178.32 t ha^{-1}) in the primary forests of Chocó is within the range of 174.23 to 541.6 t ha^{-1} reported for tropical rainforests [4], although the values are close to the lower limit. Similarly, the aboveground biomass values in Chocó are within the range of 98.2 to 295.1 t ha^{-1} reported for different types of tropical forest, but are below the average (243.8 t ha^{-1}) reported for Colombia [18]. However, the values for the tropical rainforests in Chocó are similar to the average reported by Phillips et al. [18] of

172.2 t ha^{-1} for this same type of forest. Additionally, the aboveground biomass recorded

in this study is similar to that observed in other mature forests in the region. For example, Faber-Langendoen and Gentry [10] estimated an aboveground biomass of between 178.1 and 210.9 t ha^{-1} in the forests of Tutunendo and Bajo Calima. In general, the results show that the aboveground biomass in the Chocó rainforests has intermediate values compared with other types of tropical rainforest.

In the secondary forests that were previously affected by open-pit mining in Chocó, with successional ages of 15 and 30 years, the average aboveground biomass was 35.17 and 56.3 t ha^{-1} (45, 7 t ha^{-1} average), respectively, which is within the range of 20 to 225 t ha^{-1} (average of 121.8 t ha^{-1}) reported for secondary tropical forests after 20 years of succession [7]. The aboveground biomass is 27% of that of a mature forest at this successional age; this value would reach 90% after 66 years [7]. The AB in secondary forests was recorded as being up to 52% of that of a primary forest after 20 years of recovery [8].

In this study, the AB in the forests 20 years after mine closure was as high as 40.65 t ha^{-1}, corresponding to 22.8% of the aboveground biomass of a mature forest in the region. After 30 years of succession, 31% of the aboveground biomass of a primary forest was reached in the region. That is, the aboveground biomass of a primary forest will be reached in 95 years if the rate of carbon accumulation in the ecosystem degraded by mining remains constant. However, previous modeling showed that these ecosystems can take more than 300 years to reach an aboveground biomass similar to that of the primary forests in the region [13]. This shows that in areas degraded by mining, the accumulation of aboveground biomass tends to be slower than that in secondary forests that have been affected by other types of disturbances, such as agriculture, logging, and/or livestock [7,19].

We found that the areas degraded by mining captured less carbon by comparing the aboveground biomass accumulation rate of 3.05 t ha^{-1} $year^{-1}$ in tropical secondary forests after 20 years of succession after use for agriculture and livestock [7], with those recorded in forests degraded by mining in Chocó of 2.34 and 1.87 t ha^{-1} $year^{-1}$ in forests after 15 and 30 years of succession, respectively. This finding aligns with those reported by Quinto et al. [13] in other localities in Chocó, and Kalamandeen et al. [19] for Amazon mining areas. Furthermore, the reduced carbon capture rate of this type of ecosystem is corroborated by the tropical rainforests in the region accumulating aboveground biomass at

7.8 to 10.9 t ha^{-1} $year^{-1}$ [11]. In summary, mining substantially affected the accumulation

of carbon in the ecosystem, weakening the role of the ecosystem in mitigating the effects of climate change.

1.1. *Influence of Environmental Factors on Aboveground Biomass in Forests and Areas Degraded by Mining in Chocó*

The differences in the aboveground biomass depended on the type of forest, succession time, and location in the Chocó forests, similar to what was reported by Poorter et al. [7], Kalamandeen et al. [19], and Oberleitner et al. [8]. The aboveground biomass was determined by the type of ecosystem, average tree diameter, species richness, abun- dance of individuals, Shannon's equity, and Margalef diversity at the general level. These results are similar to those reported by Poorter et al. [6], who found that the amount of aboveground biomass was strongly dependent on precipitation, average tree diameter, and species diversity in an analysis at the neotropical forest scale; aboveground biomass was weakly related to soil [6]. Additionally, Chisholm et al. [20] observed a positive relationship between aboveground biomass and tree species diversity. A greater species richness likely increases the variation in the characteristics of the species present in a community, which results in niche complementarity, high resource capture, increased efficiency in resource use, high productivity [6], and, consequently, a greater aboveground tree biomass. In summary, tropical forest ecosystems that have large trees (diameter) and with greater species diversity tend to accumulate more carbon.

Aboveground biomass was previously found to be directly related to the structural characteristics of the forest, such as the basal area, abundance of individuals, tree height, tree crown size, wood density, and abundance of large trees [6]. For example, in a study carried out on pantropical forests, 70% of the variation in aboveground biomass was found to be due to the abundance of large trees (DBH > 70 cm) [21], showing the importance of not only the abundance of individuals but also their sizes. These results align with our observations because aboveground biomass was significantly related to structural variables such as average tree diameter and the abundance of individuals. Consequently, tree diameter in particular appears to be related to the aboveground biomass because of being one of the variables used in the allometric determination, as well as the tree height and density of the wood, of aboveground biomass [16]. Consequently, tree diameter is one of the variables that best explains aboveground biomass [6]. Another important aspect to consider is that the region's forests receive high amounts of precipitation (8000 mm annually); the modeling of Poorter et al. [6] estimated a decrease in aboveground biomass within this context. This would explain the relatively low levels of aboveground biomass(178.32 t ha^{-1}) recorded in the primary forests in the region.

High levels of precipitation produce a lower aboveground tree biomass [6], because rain increases cloudiness and reduces solar radiation. In addition, excessive precipitation tends to decrease the net primary aboveground productivity of tropical forests [22], thereby reducing the aboveground tree biomass. According to Austin and Vitousek [23], high precipitation levels reduce the amount of nutrients and soil fertility, which reduces the carbon capture rate of ecosystems, because productivity is positively related with soil fertility [24–26]. For example, Paoli et al. [25] found that carbon sequestration in tropical forest ecosystems increases with soil nutrient availability. Aragão et al. [24] reported that the carbon sequestration (total and fine roots) of the tropical forests in the Amazon increases with soil P content. Similarly, Cleveland et al. [26] reported that P availability positively influences the carbon sequestration rates in tropical humid forests. These findings could explain the relatively low aboveground biomass in some of the Chocó forests, as the soils have low nutrient contents. Although the physicochemical characteristics of the soil were not significantly related to aboveground biomass, as evidenced in other tropical forests [6], the weak relationship with edaphic conditions occurred because many of the tree species present in these forests are adapted to nutrient-poor soils, and spatial changes in their content and edaphic availability do not produce strong variations in aboveground biomass. In areas previously degraded by mining, AB was found to be positively related to species richness and Shannon evenness, and negatively related to Margalef diversity and the soil's silt content. These findings are similar to those reported by Oberleitner et al. [8], who found that aboveground biomass is positively related to the age of the substrate and forest cover, and negatively related to species richness in secondary forests in Costa Rica. Asner et al. [5] observed that aboveground biomass amounts are positively affected by poor soil drainage, precipitation, altitude, the dominant species composition, and substrate age in tropical rainforests in Hawaii [5]. The dominance of some tree species (*Philodendron acutatum*, *Cespedesia spathulata*, and *Croton chocoanus*) adapted to recovering areas leads to the aboveground biomass amount being inversely proportional to species richness, especially in areas with high toxic aluminum contents, where most species do not properly develop. This is likely to occur in the areas degraded by mining considered in this study, as the soils have high aluminum contents.

In forested areas degraded by mining, the aboveground biomass was not only related to tree diversity, but also to the soil's silt content. This result aligns with that reported by Kalamandeen et al. [19], who stated that the recovery of biomass in areas deforested by min- ing is strongly conditioned by soil nutrient contents, especially nitrogen. Poorter et al. [7] observed that the recovery of aboveground biomass in secondary forests is related to water availability, forest cover, previous land use, and soil fertility in terms of cation exchange capacity (CEC), which shows the importance of the soil in the recovery of aboveground biomass in ecosystems previously degraded by mining. Furthermore, in mining areas, soil is generally removed, and a new substrate is generated that needs to be colonized, which is why the AB produced during primary succession [13,19] requires longer to reach that of a primary forest. All of the above results show the importance of environmental, structural, and biological factors in the accumulation of aboveground biomass and carbon in primary tropical forests and in succession (recovery) processes.

In conclusion, the carbon capture and storage in the Chocó forests is directly related to factors such as species diversity, tree size, soil, forest type, successional age, and previous use of the ecosystem, among others. As such, biodiversity conservation programs should be developed through initiatives such as the reduction in greenhouse gas emissions from deforestation and forest degradation (REDD+) projects [3], which provide comprehen- sive co-benefit strategies in which species and ecosystems are conserved to substantially contribute to the mitigation of the effects of climate change, as well as to the sustainable development of rural communities in the region.

Supplementary Materials

The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/life15010098/s1, Table S1: Analysis of Variance for Aboveground biomass.

Author Contributions: Conceptualization: D.P.A. (lead). Data curation: D.P.A. (equal) and H.Q.M. (equal). Formal analysis: D.P.A. (equal) and H.Q.M. (equal). Investigation: D.P.A. (equal), H.Q.M. (equal) and J.M.D.A. (equal). Methodology: D.P.A. (equal), H.Q.M. (equal) and J.M.D.A. (equal). Project administration: H.Q.M. (lead). Resources: D.P.A. (equal) and H.Q.M. (equal). Writing—original draft: D.P.A. (equal), H.Q.M. (equal) and J.M.D.A. (equal). Writing—review and editing: D.P.A. (equal), H.Q.M. (equal) and J.M.D.A. (equal). All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded from resources of the project titled: Evaluación del efecto de la fertilización del suelo sobre la producción neta del ecosistema en áreas degradadas por minería, como estrategia para potenciar la captura de carbono y la venta de servicios ambientales en el Chocó Biogeográfico (CÓDIGO 1128-852-72243), presented by the Technological University of Chocó "D.L.C.", the National University of Colombia, Medellín headquarters, the University of Valladolid (Spain), the John Von Neumann Pacific Environmental Research Institute—IIAP, and the SENA Chocó, and approved by the Ministry of Science, Technology and Innovation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data is available in Supplementary Materials.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities.

Nature **2000**, *403*, 853–858. [CrossRef] [PubMed]

2. Pan, Y.; Birdsey, R.A.; Phillips, O.L.; Jackson, R.B. The Structure, Distribution, and Biomass of the World's Forests. *Annu. Rev. Ecol. Evol. Syst.* **2013**, *44*, 593–622. [CrossRef]

3. Intergovernmental Panel on Climate Change (IPCC). *Climate Change 2014: Synthesis Report*; Core Writing Team, Pachauri, R.K., Meyer, L.A., Eds.; Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; IPCC: Geneva, Switzerland, 2014; p. 151.

4. Chave, J.; Condit, R.; Muller-Landau, H.C.; Thomas, S.C.; Ashton, P.S.; Bunyavejchewin, S.; Co, L.L.; Dattaraja, H.S.; Davies, S.J.; Esufali, S.; et al. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol.* **2008**, *6*, e45. [CrossRef]

5. Asner, G.P.; Hughes, R.F.; Varga, T.A.; Knapp, D.E.; Kennedy-Bowdoin, T. Environmental and biotic controls over aboveground biomass throughout a tropical rainforest. *Ecosystems* **2009**, *12*, 261–278. [CrossRef]

6. Poorter, L.; van der Sande, M.T.; Thompson, J.; Arets, E.J.M.M.; Alarcón, A.; Álvarez-Sánchez, J.; Ascarrunz, N.; Balvanera, P.; Barajas-Guzmán, G.; Boit, A.; et al. Diversity enhances carbon storage in tropical forests. *Glob. Ecol. Biogeogr.* **2015**, *24*, 1314–1328. [CrossRef]

7. Poorter, L.; Bongers, F.; Aide, T.M.; Almeyda Zambrano, A.M.; Balvanera, P.; Becknell, J.M.; Boukili, V.; Brancalion, P.H.S.; Broadbent, E.N.; Chazdon, R.L.; et al. Biomass resilience of Neotropical secondary forests. *Nature* **2016**, *530*, 211–214. [CrossRef] [PubMed]

8. Oberleitner, F.; Egger, C.; Oberdorfer, S.; Dullinger, S.; Wanek, W.; Hietz, P. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. *For. Ecol. Manag.* **2021**, *479*, 118580. [CrossRef]

9. Poveda, I.C.; Rojas, C.; Rudas, A.; Rangel, O. El Chocó biogeográfico: Ambiente Físico. In *Colombia Diversidad Biótica IV. El Chocó*

biogeográfico/Costa Pacífica; Rangel, O., Ed.; Instituto de Ciencias Naturales, Universidad Nacional de Colombia sede Bogotá: Santa Fe de Bogotá, Colombia, 2004; pp. 1–21.

10. Faber-Langendoen, D.; Gentry, A. The structure and diversity of rain forests at Bajo Calima, Chocó Region, Western Colombia. *Biotropica* **1991**, *23*, 2–11. [CrossRef]

11. Quinto-Mosquera, H.; Moreno, F. Net Primary Productivity and Edaphic Fertility in Two Pluvial Tropical Forests in the Chocó Biogeographical Region of Colombia. *PLoS ONE* **2017**, *12*, e0168211. [CrossRef]

12. Instituto de Investigaciones Ambientales del Pacífico IIAP. *Plan Integral de Cambio Climático del Departamento del Chocó (PICC-Chocó)*; Ministerio de Ambiente y Desarrollo Sostenible, Instituto de Investigaciones Ambientales del Pacífico IIAP: Quibdó, Colombia, 2015; 211p.

13. Quinto-Mosquera, H.; Cuesta-Nagles, J.; Mosquera-Sánchez, I.; Palacios-Hinestroza, L.; Peñaloza, H. Biomasa vegetal en zonas degradadas por minería en un bosque pluvial tropical del Chocó Biogeográfico. *Rev. Biodivers. Neotrop.* **2013**, *3*, 53–64. [CrossRef]

14. Quinto-Mosquera, H.; Hurtado, D.; Arboleda, J. Influencia de las condiciones edáficas sobre la dominancia y diversidad de árboles en bosques pluviales tropicales del Chocó biogeográfico. *Rev. Biol. Trop.* **2019**, *67*, 1278–1291. [CrossRef]

15. Baker, T.R.; Phillips, O.L.; Malhi, Y.; Almeida, S.; Arroyo, L.; Di Fiore, A.; Erwin, T.; Killeen, T.J.; Laurance, S.G.; Laurance, W.F.; et al. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Chang. Biol.* **2004**, *10*, 545–562. [CrossRef]

16. Álvarez, E.; Duque, A.; Saldarriaga, J.; Cabrera, K.; de las Salas, G.; del Valle, I.; Lema, A.; Moreno, F.; Orrego, S.; Rodríguez, L. Tree aboveground biomass allometries for carbon stocks estimation in the natural forests of Colombia. *For. Ecol. Manag.* **2012**, *267*, 297–308. [CrossRef]

17. R Development Core Team. *R: A Language and Environment for Statistical*

Computing; R Foundation for Statistical Computing: Vienna, Austria, 2012.

18. Phillips, J.F.; Duque, A.J.; Yepes, A.P.; Cabrera, K.R.; García, M.C.; Navarrete, D.A.; Álvarez, E.; Cárdenas, D. *Estimación de las Reservas Actuales (2010) de Carbono Almacenadas en la Biomasa Aérea en Bosques Naturales de Colombia. Estratificación, Alometría y Métodos Analíticos*; Instituto de Hidrología, Meteorología, y Estudios Ambientales—IDEAM: Bogotá, Colombia, 2011; 68p.

19. Kalamandeen, M.; Gloor, E.; Johnson, I.; Agard, S.; Katow, M.; Vanbrooke, A.; Ashley, D.; Batterman, S.A.; Ziv, G.; Holder-Collins, K.; et al. Limited biomass recovery from gold mining in Amazonian forests. *J. Appl. Ecol.* **2020**, *57*, 1730–1740. [CrossRef]

20. Chisholm, R.A.; Muller-Landau, H.C.; Rahman, K.A.; Bebber, D.P.; Bin, Y.; Bohlman, S.A.; Bourg, N.A.; Brinks, J.; Bunyavejchewin, S.; Butt, N.; et al. Scale-dependent relationships between tree species richness and ecosystem function in forests. *J. Ecol.* **2013**, *101*, 1214–1224. [CrossRef]

21. Slik, J.W.F.; Paoli, G.; McGuire, K.; Amaral, I.; Barroso, J.; Bastian, M.; Blanc, L.; Bongers, F.; Boundja, P.; Clark, C. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob. Ecol. Biogeogr.* **2013**, *22*, 1261–1271. [CrossRef]

22. Schuur, E.A. Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology* **2003**, *84*, 1165–1170. [CrossRef]

23. Austin, A.; Vitousek, P. Nutrient dynamics on a precipitation gradient in Hawaii. *Oecologia* **1998**, *113*, 519–529. [CrossRef] [PubMed]

24. Aragão, L.E.O.; Malhi, Y.; Metcalfe, D.B.; Silva-Espejo, J.E.; Jiménez, E.; Navarrete, D.; Almeida, S.; Costa, A.C.L.; Salinas, N.; Phillips, O.L.; et al. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* **2009**, *6*, 2441–2488. [CrossRef]

25. Paoli, G.D.; Curran, L.M.; Zak, D.R. Phosphorus efficiency of aboveground productivity in Bornean rain forest: Evidence against the unimodal efficiency hypothesis. *Ecology* **2005**, *86*, 1548–1561. [CrossRef]

26. Cleveland, C.C.; Townsend, A.R.; Taylor, P.; Alvarez-Clare, S.; Bustamante, M.; Chuyong, G.; Dobrowski, S.Z.; Grierson, P.; Harms, K.E.; Houlton, B.Z.; et al. Relationships among net primary productivity, nutrients and climate in tropical rain forest: A pan-tropical analysis. *Ecol. Lett.* **2011**, *14*, 939–947. [CrossRef] [PubMed]

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Artículo 2

Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian. Pacific.

Revista Brasileira de Ciéncia do Solo. 2024;48:e0230053. https://doi.org/10.36783/18069657rbcs20230053

Harley Quinto Mosquera[8] , **Hamleth Valois Cuesta**[9] and **David Pérez Abadía**[10]

Abstract.

Tropical forests have the highest rates of net primary productivity (NPP) in terrestrial ecosystems and, therefore, may contribute significantly to the mitigation of global climate change. Although NPP is influenced by soil fertility, and recently, in some regions, mining activity in forest ecosystems has intensified. Little is known about how soils determine the restoration of NPP in forests degraded by mining. We evaluated the influence of soil nutrients on wood NPP of post-mining forests in the biogeographic Chocó region (Colombia), with emphasis on the effects of nitrogen (N) and phosphorus

(P) limitations in post-mining forests under successional stages of 12-15 or 30-35

[8]) **Harley Quinto Mosquera** Universidad Tecnológica del Chocó Diego Luis Córdoba, Facultad de Ciencias Naturales, Programa de
Biología, Departamento del Chocó, Ciudad de Quibdó, República de Colombia
Universidad de Valladolid, Instituto Universitario De Investigación en Gestión Forestal Sostenible, Programa de Conservación y Uso Sostenible de Sistemas Forestales, Palencia, España.

[9] **Hamleth Valois Cuesta** Universidad de Valladolid, Instituto Universitario De Investigación en Gestión Forestal Sostenible, Programa de Conservación y Uso Sostenible de Sistemas Forestales, Palencia, España.

[10]) **David Pérez Abadía** 5 y 6

years. For this, permanent plots were established in secondary post-mining forests in Jigualito (Colombian Pacific), the wood NPP (accumulated and current) was evaluated, and it was related to soil properties such as organic matter (OM), acidity, Al, total N, available P, magnesium (Mg), potassium (K), calcium (Ca), and texture. An accumulated wood NPP of 0.72 t ha^{-1} yr^{-1} was recorded in post-mining forests 12-15 years old. Meanwhile, in post-mining forests of 30-35 years, the accumulated wood NPP was 6.52 t ha^{-1} yr^{-1}. The current wood NPP was 4.25 t ha^{-1} yr^{-1} in post-mining forests with 30-35 years of recovery. Accumulated NPP positively correlated with soil OM, total N, Ca, Mg, and effective cation exchange capacity–ECEC in post-mining forests. In post-mining forests, a slow recovery of the wood NPP was denoted in the first years. Soil nutrients determined the wood NPP, and a multiple limitation of nutrients with the succession was observed, which corroborates the need to restore the degraded ecosystem in the region.

Keywords: biogeographic Chocó, global climate change, nutrient limitation, restoration, succession.

Introduction

Tropical forests are considered the most important terrestrial ecosystem in terms of net primary productivity (NPP) and have a key role as sinks and reservoirs of atmospheric carbon (Phillips et al., 1998; Clark et al., 2001b; Grace, 2004; Pan et al., 2011). Specifically, it has been estimated that these forests store about 40 % of the existing carbon in the terrestrial ecosystems of the planet (Dixon et al., 1994), they represent 36 % of the global NPP (Field et al., 1998; Beer et al., 2010) and capture about 1.19 petagrams of carbon annually (Pg C yr^{-1}) (Pan et al., 2011), thus contributing significantly to carbon fixation and balance, and global climate change mitigation (Grace, 2004; IPCC, 2014). Consequently, there is a growing interest in evaluating the NPP of these forests, and the environmental and anthropic factors that determine it (Phillips et al., 1998; Clark et al., 2001a; Malhi et al., 2004; IPCC, 2014).

Several studies have documented that the NPP of tropical forests is influenced by factors such as precipitation, climate, solar radiation, temperature, soil type and its fertility, as well as by other factors related to the dynamics (disturbances) of the ecosystem, structure and species composition (Schuur, 2003; Del Grosso et al., 2008, Jiménez et al., 2009; Cleveland et al., 2011; Malhi et al., 2011; Wu et al., 2011; van der Sande et al., 2018; Linger et al., 2020); for this reason, a wide range of aboveground NPP has been shown in tropical rainforests, between 1.2 and 15.2 Mg ha^{-1} yr^{-1} (Clark et al., 2001b).

Soil nutrient content has shown a positive effect on NPP of tropical forests (Alvarado and Raigosa, 2012; van der Sande et al., 2018). In this sense, it has been determined nutrients tend to be more correlated with NPP are N, P, K and Ca (Paoli and Curran, 2007; Cleveland et al., 2011); which are part of the nutrients considered physiologically essential for plant growth (Lambers et al., 2008a). For example, Vitousek (1984) conducted an analysis of N, P and Ca recycling and determined the availability of P, but not N, limited the litter production (a component of the NPP). Meanwhile, Paoli and Curran (2007) observed that the NPP of tropical forests increased with the availability of P, N, K, Ca, Mg, and ECEC. Similarly, Aragão et al. (2009) reported Amazon's NPP (total and fine roots) increases significantly with the P content of the soil. Likewise, some years ago, in a meta-analysis on NPP in tropical forests, Cleveland et al. (2011) reported P availability positively influences the NPP rates. On the other hand, Quinto et al. (2017) observed that the production of leaves and fine roots increased with soil fertility in forests of the biogeographic Chocó. In summary, these studies show the importance of soil nutrients on NPP and mitigating global climate change.

However, in recent decades, tropical forests have been severely deforested and degraded due to human activities such as logging, agriculture, cattle ranching, and mining, among others (Primack, 2008), which affect the ability of these ecosystems to mitigate global climate change (Grace, 2004; IPCC, 2014). Particularly, open-pit mining strongly impacts the NPP, once vegetation and soil covers are removed (Diaz and Elcoro, 2009; Valois, 2016; Maus et al., 2022; Giljum et al., 2022). Not only soil and vegetation are affected, but all the ecological processes of the ecosystem (Holl, 2002; ELAW, 2010). In this sense, with mining, there is a reduction in the capture of atmospheric CO_2 due to the loss of vegetation, the carbon balance is altered, and CO_2 emissions into the atmosphere increase, which accentuates global warming (ELAW, 2010). It is estimated that from 2001 to 2013, about 1680 km^2 of South American tropical forests were lost (Primack and Vidal, 2019), with threatening effects not only to the region's biodiversity, but also to soil organic carbon (SOC) and to the capacity of ecosystems to mitigate global climate change.

This situation is currently taking place in Colombia, in the Chocó (Colombian Pacific) department, where open-pit gold mining is damaging soil and rivers of the natural ecosystems (Valois, 2016). Nonetheless, about 840 thousand hectares of mature forest were recently granted licenses for mining exploitation in the territory (Ángel et al., 2019). Now, it is necessary to develop restoration projects and programs to recover the functionality and NPP of the ecosystem. Knowing the environmental factors that limit the NPP of post-mining ecosystems is necessary to achieve this purpose.

In this sense, Kalamandeen et al. (2020) reported an increase in NPP of post-mining forests in the Amazon, in areas where soil had higher N content, denoting the influence of soil nutrients on the restoration of degraded ecosystems. Likewise, it has been hypothesized that, in tropical soils, in initial successional stages, there is a limitation of the NPP by N, which over time is mitigated due to colonization of plants with capacity to fix atmospheric N_2 symbiotically (Walker, 1993). Therefore, in the ecosystem, to the extent that there is a greater colonization of N-fixing plants, and succession advances, this limitation of the NPP would be reduced (Cleveland et al., 1999; Walker and del Moral, 2008). Unlike N, the levels of soil P tend to be high in the first successional stages, and over time, its availability to plants tends to decrease due to losses by leaching and immobilization in Fe and Al oxides (Walker and Syers, 1976; Vitousek et al., 2010). With this, a limitation of the NPP is expected due to low availability of P in advanced successions and mature forests (Vitousek, 1984).

Based on the above discussion and taking into account that the region is one of the most biodiverse on the planet (Rangel, 2004), and has one of the highest levels of precipitation (Poveda et al., 2004); that possibly affects the edaphic limitation and availability of nutrients due to leaching (Austin and Vitousek, 1998; Posada and

Schuur, 2011; Quinto and Moreno, 2016); this study aimed to evaluate the soil nutrients influence on the wood NPP of post-mining forests in the biogeographic Chocó, and, contribute with experimental elements to the restoration of the NPP of these degraded ecosystems.

Materials And Methods

Study area

This study was carried out in forested areas previously degraded by open-pit gold mining, in the locality of Jigualito (5° 06’ 01” N - 76° 32’ 44” W), in the municipality of Condoto, department of Chocó, Colombia. Average annual precipitation is 8000 mm, the mean annual temperature is 26 °C, and altitude is 70 m with flat topography. This locality is part of the biogeographic subregion of North Central Chocó, which includes the upper basins of the Atrato and San Juan rivers, in Piedemonte and Colinas lowland landscape units with humid soils and a type of transitional sedimentary rock (Poveda et al., 2004). The localities lie within the Tertiary Sedimentary Hills geomorphological unit formed by low-altitude sedimentary rocks composed of sandy clayey, sandstone and limestone. The forests are mostly secondary, with different recovery ages since mining has been carried out in the area at different times.

Soils of the post-mining forests are Alisols (WRB) or Ultisols (Soil Taxonomy) and, due to mining, they have rocky material and sand. The A horizon was removed during mining, with irregular return of organic material after mining. In addition, they are acidic and have high OM, total N, available P, Al and clay contents; while the contents of Ca, K, Mg, ECEC and silt are low (Quinto et al., 2022). In these forests, the most dominant tree species are *Cecropia peltata, Vismia baccifera, Cosmibuena macrocarpa, Ochroma pyramidalis, Welfia regia, Pityrogramma calomelanos, Cespedesia spathulata, Inga chocoensis,* and *Pourouma bicolor* (Ramírez and Rangel, 2019).

This study assessed two post-mining forests with different succession times. These forests were secondary forests that grew in abandoned illegal mining areas.

The first post-mining forest was 12-15 years old (F12-15) and the second forest was 30-35 years old (F30-35), being that the time of restoration after mining ended. In the post-mining forests F12-15, 103 plots of 5 × 5 m (25 m^2) were installed as NPP sampling units; while in the forests F30-35, 37 plots of 10 × 10 m (100 m^2) were installed. Plot size and replicates in each forest were different due to irregular site characteristics, which only allowed sampling in this way.

Physical and chemical soil properties

In each plot (103 and 37 in the post-mining forest of 12-15 and 30-35 years, respectivity), composite samples of soil were taken at a depth of 0.20 m, to which the parameters of acidity (pH), aluminum content (Al), organic matter (OM), total N, available P, calcium (Ca), potassium (K), magnesium (Mg), effective cation exchange capacity (ECEC), and texture (percentages of sand, silt, and clay), according to the following laboratory techniques: Bouyoucos for textural fractions, potentiometric in water solution (1:2) for pH, Walkley and Black for OM, Micro- Kjeldahl for total N, ascorbic acid in an UV-VIS spectrophotometer after extraction with the Bray II method for available P, atomic absorption for Ca, Mg, and K extracted with ammonium acetate, described in Osorio (2014), and Quinto et al. (2022). Soil sampling was carried out in 2020 and 2021.

Diameters and height of trees

In the installed plots, the sampling criteria for the forest inventory was stratified sampling by succession time forests; here the circumference at breast height (1.30 m above ground level) was measured with a measuring tape in all trees with circumference >31.4 cm (Diameter at breast height- DBH >10 cm) in each quadrat; subsequently, the circumference values were transformed to DBH. The perimeter of the tree trunk where the DBH was measured was marked with yellow paint to ensure that subsequent measurements were made in the same strip as the first measurement. Measurement of tree heights was carried out with a Clinometer at fixed distances of 15 m from the tree. All measured trees were marked with aluminum plates.

Additionally, growth habits were identified, and the characteristics of each individual were recorded. Trees were measured each August of 2020, 2021 and 2022 in F30-35; while in F12-15, inventories were carried out only in 2020 due to armed conflicts in the area. In total, 114 trees were excluded from the analysis because they died during the sampling period.

Botanical identification

Trees were identified at the highest possible taxonomic level (species, genus, botanical family) in the herbarium of the Technological University of Chocó "Herbario Chocó". This identification was made using the specialized key of Gentry (1993), and the scientific names of species and families were corroborated on the "Tropicos" website. (https://www.tropicos.org/home). This taxonomic information was used to determine the wood density.

Wood density

We used values published in two international databases of wood density obtained for tropical forests (Brown, 1997; Baker et al., 2004). In case a species or genus found in the plots was not reported in these databases, the average of the genus or family of the species was used.

Aboveground biomass and wood net primary productivity (wood NPP)

The allometric model proposed by Álvarez et al. (2012) (Equations 1, 2 and 3), based on data from the same region, was used to determine the trees' aboveground biomass (AB).

$$AB \text{ (kg)} = \exp\{-2.889 + ln[(DBH^2) \times H \times \rho]\} \quad \text{Eq. 1}$$

Current *wood NPP* = (final AB – initial AB)/ timeEq. 2
in years

Accumulated *wood NPP* = AB/the succession time in years Eq. 3

In which: AB is the aboveground biomass in kilograms; DBH is the diameter in cm; H is the height of the tree in m; ln is the natural logarithm; and ρ is the wood density. Aboveground biomass was determined at the ecosystem, species, and tree individual levels. The AB was estimated by applying harvest-based allometric regression equations to measurements of the diameters of all trees in a plot that are above the minimum size, and was expressed in tons per hectare (Mg ha^{-1}) (Clark et al., 2001a). *Current wood NPP* (2) was estimated from two successive stand-level AB estimates; that is to say, the annual increment of the AB was used, which was determined as the final AB of the trees, minus the initial AB, divided by time in years (Clark et al., 2001a). These determination of the *Current wood* NPP could only be carried out in F30-35. Meanwhile, the *Accumulated wood* NPP (3) was calculated as the AB divided by the succession time, in years (Silver et al., 2000). Wood NPP values were expressed in tons per hectare per year (Mg ha^{-1} yr^{-1}) (Clark et al., 2001a). The NPP includes not only the growth of primary producers (biomass accumulation and tissue turnover above and belowground in terrestrial ecosystems) but also the C transfer to herbivores and root symbionts (for example, mycorrhizal fungi), the excretion of organic C from algae, and the production of root exudates and plant volatile organic compounds (VOCs) (Clark et al., 2001a).

Statistical analysis

Assumptions of normality and homogeneity of variances were first evaluated with Bartlett, Hartley and Kurtosis statistical tests (between + 2.0 and -2.0). Data distribution was evaluated for each treatment using the Shapiro-Wills statistical test. Initially, mean values of wood NPP between post-mining forests (12-15 years vs 30-35 years) was compared with the Mann-Whitney (MW) test because the data did not meet the normality assumption and did not present a normal distribution (Hoshmand, 1998). The wood NPP and soil data were log-transformed whenever possible to achieve a normal distribution. Subsequently, to determine the relationship between wood NPP and soil physical and chemical properties, General Linear Models (GLM) with mixed effects, Spearman rank correlation analysis, and linear regression models (Hoshmand, 1998) were used. Spearman analyses were performed for each of the post-mining forests, and then the two post-mining forests were taken as a single ecosystem. Meanwhile, the General Linear Models (GLM) and the Linear Regression Models were carried out taking the post-mining forests as a single forest ecosystem, due to the geographic proximity and the floristic and structural similarity (Ramírez and Rangel, 2019). Analyses were performed in the R programming environment (R Development Core Team, 2013).

Results

Post-mining forests between 12-15 years of succession presented a mean NPP of 0.72 ± 0.13 Mg ha^{-1} yr^{-1} (± standard error), while in post-mining forests between 30-35 years old, the wood NPP was 6.52 ± 0.64 Mg ha^{-1} yr^{-1} (table 1). Among these post-mining forests, there were statistically significant differences in the accumulated wood NPP (MW = -8.5; p = 0.0001) (Table 1). For its part, the current wood NPP was 4.25 ± 0.8 Mg ha^{-1} yr^{-1} in post-mining forests with 30-35 years of recovery (Table 1).

On the other hand, when evaluating the post-mining forests as a single ecosystem, it was denoted by the GLM that OM, Ca, and Mg contents were significantly related to the accumulated wood NPP, and those soil properties explained 40.6 % of its variation (R^2 = 40.6 %) (table 2). For its part, Spearman's correlation showed that the accumulated wood NPP was positively and significantly related to Al, OM, total N, available P, Ca, Mg, and ECEC; while, with pH and clay, the relationship was negative (Table 3). Likewise, it was noted that the accumulated wood NPP presented the highest correlations with OM (R^2 = 25 %), Ca (R^2 = 23 %), Mg (R^2 = 14.4 %), total N (R^2 =11.4 %), and ECEC (R^2 = 23 %) (Figure 1).

Tabla 6 Aboveground biomass and wood net primary productivity of two post minigng forests in the Colombian

Post-mining forest type	N	Aboveground biomass	Cumulative wood NPP		Current wood NPP	
			Means ± SE	Range	Means ± SE	Range
		Mg ha^{-1} yr^{-1}		Mg ha^{-1} yr^{-1}		Mg ha^{-1} yr^{-1}
12-15 years	103	9.44 b ± 1.7 b	0.72 ± 0.13 *b*	0.01 - 9.82		
30-35 years	37	180.28 a ± 22.7 a	6.52 ± 0.64 *a*	0.12 - 19.23	4.25 ± 0.8	0.01 - 20.48
Mann-Whitney Test		-8.75***	-8.55***			

Means ± standard error; NPP is the net primary productivity in tons per hectare per year (t ha^{-1} yr^{-1}), the letters *a* and *b* indicate significant differences between the medians. Asterisks indicate statistically significant differences *: p<0.05; **: p<0.01; ***: p<0.001. SE is the standard error.

Finally, a very weak negative correlation with Mg was evidenced when evaluating the wood NPP of post-mining forests with 12-15 years of recovery (Table 3). Meanwhile, the accumulated wood NPP of 30-35 years post-mining forests showed a negative correlation with the total N (Table 3). For its part, the current wood NPP of post-mining forests of 30-35 years of recovery showed a negative and not significant correlation with sand, but, positive and also insignificant with silt and clay (Table 3).

Discussion

Carbon sequestration in post-mining secondary forests

Wood NPP of post-mining secondary forests in the Colombian Pacific was between 0.01 and 9.82 Mg ha^{-1} yr^{-1}, with an average of 0.75 Mg ha^{-1} yr^{-1} in areas with ages between 12-15 years. Those figures are partially similar to those of 0.70-9.15 Mg ha^{-1} yr^{-1} reported for secondary post-mining forests in Cértegui (Chocó, Colombia), with an average of 3.51 Mg ha^{-1} yr^{-1} in areas between 1.5 and 6.0 years of restoration (Quinto et al., 2013). Likewise, such wood NPP was similar to the 0.4-5.4 Mg ha^{-1} yr-

1 reported for 3-4 years forest succession in abandoned mining areas in the Amazon (Kalamandeen et al., 2020).

Tabla 7Analysis of variance of wood net primary productivity based on the soil physicochemical properties

Source	Sum of squares	Df	Mean square	F-Ratio	p-value
Model	247.711	10	24.7711	7.00	0.0000
Residuals	360.983	102	3.53905		
Total (Corr.)	608.693	112			
		Sum of squares Tipe III			
pH	9.2308	1	9.2308	2.61	0.1094
Aluminium	3.6679	1	3.6679	1.04	0.3111
Organic matter	22.6767	1	22.6767	6.41	0.0129
Total nitrogen	1.81426	1	1.81426	0.51	0.4756
Phosphorus	3.80631	1	3.80631	1.08	0.3022
Potassium	2.16343	1	2.16343	0.61	0.4361
Calcium	86.1554	1	86.1554	24.34	0.0000
Magnesium	16.7606	1	16.7606	4.74	0.0318
Sand	0.940579	1	0.940579	0.27	0.6073
Clay	4.20319	1	4.20319	1.19	0.2784
Residuals	360.983	102	3.53905		
Total (corrected)	608.693	112			

Statistical method was General Linear Model. R^2 = 40.6 %. Therefore, it seems wood NPP of post-mining forests with less than 20 years of recovery, in the Colombian Pacific and in the Amazon (Quinto et al., 2013; Kalamandeen et al., 2020) are within the range of 0.01 to 32.7 Mg ha^{-1} yr^{-1} reported for Neotropical secondary forests (Poorter et al., 2016).

However, the 0.75 Mg ha^{-1} yr^{-1} of NPP in recent post-mining areas (12-15 years of restoration) is much lower than that of the majority of secondary tropical forests (of approximately 6.1 Mg ha^{-1} yr^{-1}) after the abandonment of activities such as cattle ranching, agriculture and logging (Silver et al., 2000; Poorter et al., 2016). For example, in the central Amazon, a wood NPP rate of 11.0 Mg ha^{-1} yr^{-1} was recorded for 14 years of recovery after the abandonment of grazing (Feldpausch et al., 2004). Likewise, in secondary forests with ten years of recovery, 5.5 Mg ha^{-1} yr^{-1} of wood NPP was obtained in another ecosystem of the same Amazonian macro-basin (Johnson et al., 2000). Those results show the influence of the type of the previous disturbance on the recovery capacity of the ecosystem (Silver et al., 2000; Guariguata and Ostertag, 2001; Chazdon et al., 2016). Specifically, it is corroborated that open-cast mining significantly affects the ecosystem, which generates a slow biomass recovery and functionality, as has been suggested in previous analyses of tropical successions (Guariguata and Ostertag, 2001).

Wood NPP of recent post-mining forests (<20 years) is low is probably due to the impact that mining has on the ecosystem. Soil organic horizon is removed, and the overall soil structure is altered, mainly leaving rocks and sand on the surface (Ramírez et al., 2019).

Tabla 8 Spearman correlations of carbon sequestration and physichemical properties of post mining forests in the Colombian Pacific

Soil	General-Cumulative wood NPP	Wood NPP (12-15 years)	Wood NPP (30-35 years)	
	Cumulative	Cumulative	Cumulative	Current
pH	-0.25	0.12	-0.05	0.05
p-value	0.003	0.209	0.758	0.767
Aluminium	0.17	-0.12	0.05	0.03
p-value	0.049	0.216	0.744	0.854
Organic matter	0.53	0.10	-0.25	-0.10
p-value	0.000	0.318	0.133	0.534
Total nitrogen	0.44	0.13	-0.36	-0.19
p-value	0.000	0.188	0.029	0.263
Phosphorus	0.21	-0.03	0.02	-0.02
p-value	0.012	0.760	0.895	0.925
Potassium	0.11	0.11	-0.19	0.04
p-value	0.194	0.275	0.259	0.789
Calcium	0.44	-0.11	-0.09	-0.20
p-value	0.000	0.273	0.605	0.221
Magnesium	0.31	-0.17	-0.09	-0.25
p-value	0.000	0.080	0.582	0.131
ECEC	0.40	-0.15	-0.06	-0.23
p-value	0.000	0.121	0.725	0.163
Sand	0.10	0.00	0.11	-0.53
p-value	0.270	0.971	0.703	0.068
Silt	-0.06	0.00	-0.02	0.52
p-value	0.509	0.963	0.939	0.071
Clay	-0.21	-0.04	-0.23	0.50
p-value	0.027	0.691	0.428	0.083

Vegetation and the soil/regolith that covers mineral deposits are removed (Diaz and Elcoro, 2009; Valois, 2016), affecting soil fertility (Quinto et al., 2022), plant biomass (Quinto et al., 2013) and many other ecological processes (Holl, 2002; ELAW, 2010), like nutrient recycling (Quinto et al., 2022) and carbon sequestration (NPP) (Kalamandeen et al., 2020). Such effects are stronger than those generated by other anthropic activities like selective felling of trees, subsistence agriculture, and grazing (Silver et al., 2000), which still preserve the organic horizon, texture, and soil nutrients (Guariguata and Ostertag, 2001).

On the other hand, the post-mining forests between 30-35 years of recovery had average wood NPP of 4.25 and 6.52 Mg ha^{-1} yr^{-1}, comparable to the report of 6.1 Mg ha^{-1} yr^{-1} for Neotropical secondary forests (Silver et al., 2000; Poorter et al., 2016), or higher than reports of 1.01 to 4.36 Mg ha^{-1} yr^{-1} for secondary rainforests between 23 and 40 years of recovery after logging in the biogeographic Chocó (Forero-Peña et al., 2022). Possibly, this increase in the wood NPP of the post-mining areas with the regeneration age is due to the increase in the edaphic content of OM and nutrients (total N, Ca, Mg, ECEC) that occurs with the succession (Quinto et al., 2022). Likewise, over the succession, there is an increase in activity, abundance, functionality (ammonification and nitrification), richness and post-mining microbial biomass (Sansupa et al., 2021). In addition, the edaphic colonization of mycorrhizae may increase (Zhang et al., 2017). In early succession

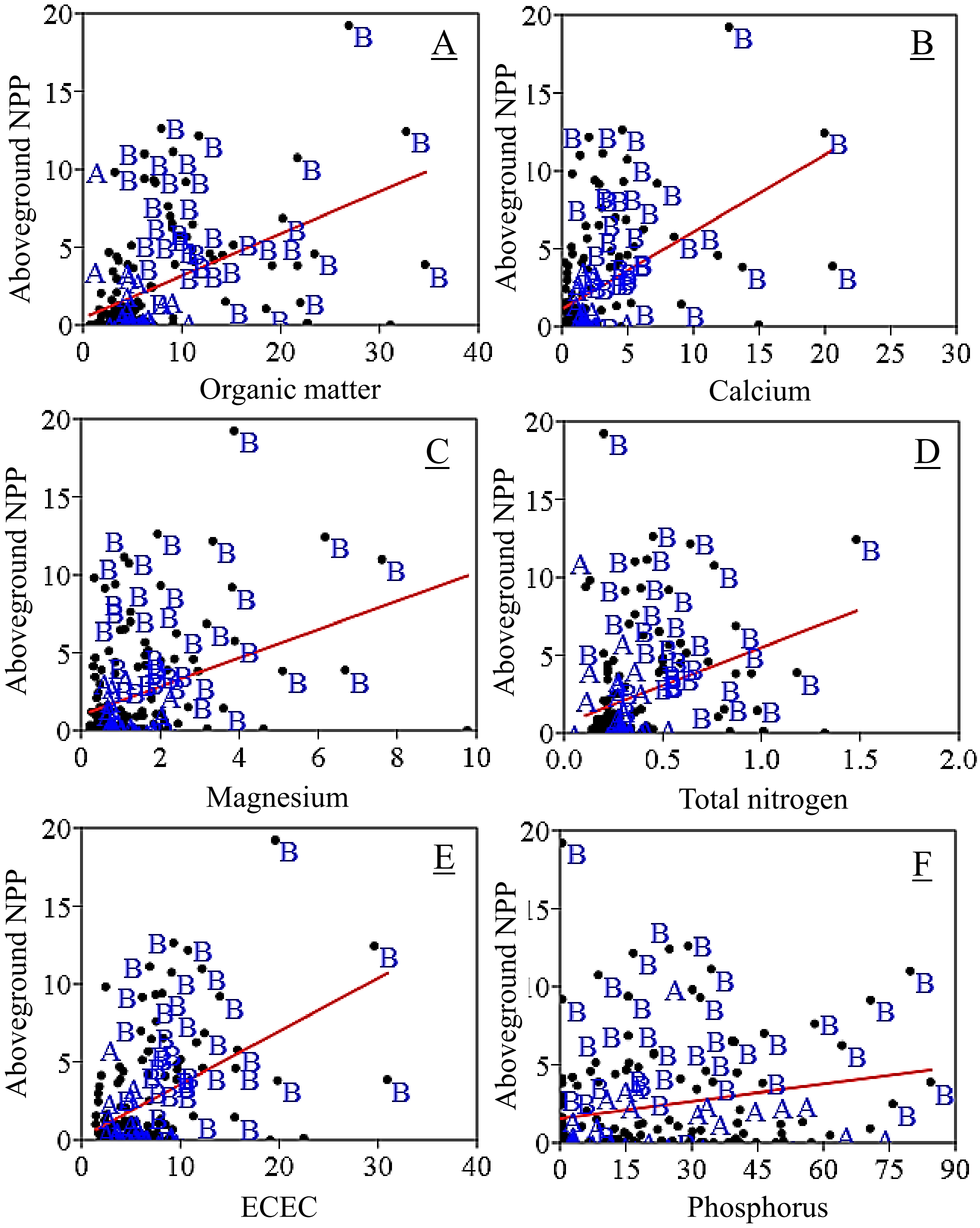

FIgura 4 Linear regressions of above ground tree net primary productivity (NPP)

and soil nutrients in post-mining forests in the Colombian Pacific. (a) Wood NPP vs Organic matter (r^2 = 25 %; p<0.0001); (b) Wood NPP vs Calcium (r^2 = 23 %; p<0.0001); (c) Wood NPP vs Magnesium (r^2 = 14.4 %; p<0.00001); (d) Wood NPP vs total Nitrogen (r^2 = 11.4 %; p = 0.00004); (e) Wood NPP vs ECEC (r^2 = 23 %; p<0.00001); (f) Wood NPP vs. Available Phosphorus (r^2 = 4.7 %; p = 0.009)

ecosystems (<20 years), the presence of mycorrhizae is low. In contrast, in post-mining forests with a longer recovery time, such as in mines >30 years of abandonment, surely the presence of arbuscular mycorrhizae and edaphic proteins related to glomalin favor recalcitrant carbon components, which benefit the accumulation of soil organic carbon (SOC) and OM in tropical forests (Zhang et al., 2017). This surely explains the higher wood NPP in these advanced succession post-mining forests.

Another factor that explains the higher wood NPP of advanced succession post-mining forests (>30 years) in the Colombian Pacific is the colonization by tree species, either pioneer or climax, that store greater amounts of carbon in a shorter time (Guariguata and Ostertag, 2001). The composition of tree species recorded in these abandoned mines were *Cecropia peltata, Vismia baccifera, Cosmibuena macrocarpa, Ochroma pyramidalis, Welfia regia, Pityrogramma calomelanos, Cespedesia spathulata, Inga chocoensis*, and *Pourouma bicolor*) (Ramírez and Rangel, 2019). Those species have been commonly reported for previously degraded ecosystems, secondary forests and areas with different stages of ecological succession (Alves et al., 1997; Guariguata and Ostertag, 2001). These species are possibly the ones with the greatest tolerance to adverse conditions (isolation, high temperatures, stress, acidity, herbivory, infertility and Al toxicity) that occur in areas degraded by mining (Diaz and Elcoro, 2009; Valois, 2016; Quinto et al., 2022). For this reason, it can be deduced that this physiological capacity contributes significantly to the wood NPP of the previously degraded ecosystem.

What influences do soil nutrient contents have on wood NPP of post-mining forests of the biogeographical region of Chocó?

Soil conditions were essential for the restoration of the wood aboveground biomass (wood AB) and wood NPP in abandoned mines in tropical regions (León and Osorio, 2014). However, in our study, the current wood NPP (Clark et al., 2001b) did not show a significant relationship with soil nutrient content variations; similar to what was observed by Oberleitner et al. (2021) in measurements of an increase in wood AB in secondary forests of Costa Rica. Likewise, Poorter et al. (2016) recorded only a significant association between the accumulation of wood AB and ECEC in tropical secondary forests. For this reason, annual changes in wood NPP of the trees could have little relationship with the spatial variation in the contents of soil nutrients. This is surely due to the fact that most trees growing on acidic and nutrient-poor soils are adapted to low nutrient availability (Whitmore, 1998; Lambers et al., 2008b), and changes in their availability generate responses. In the long term, which is not easily evidenced from one year to the next, as has happened in some studies when the tree wood NPP is evaluated in annual inventories (Aragão et al., 2009; Cleveland et al., 2011; Quinto and Moreno, 2017; Oberleitner et al., 2021); as it happens in this study carried out in post-mining forests.

On the other hand, in the accumulated wood NPP, calculated as the wood AB divided by the succession age in years (Silver et al., 2000), a positive relationship was evidenced between the wood NPP and soil nutrients (OM, total N, Ca, Mg, and ECEC) in post- mining forests, which together show that small soil patches of higher fertility tend to facilitate carbon accumulation and the recovery of ecosystem functionality. Such wood NPP rate observed in more fertile soils of abandoned mines is similar to that reported by Kalamandeen et al. (2020), who reported a higher wood NPP in abandoned mines with higher total N content. Likewise, Poorter et al. (2016) determined that the percentage of AB accumulation is determined by soil fertility (CEC) in Neotropical secondary forests in different successional stages. Likewise, Tucker et al. (1998), in secondary forests with more than 15 years of succession, compared the recovery of the basal area (indirect measure of the forest biomass) in fertile and nutrient-rich soils, with the recovery on infertile soils, Oxisols; and found that in fertile soils the basal area was much greater over the succession time, and in such forest, the AB of a primary forest was reached more quickly (Tucker et al., 1998). Thus, the positive influence of edaphic fertility on wood NPP in tropical forests is evidenced (Moran et al., 2000; Guariguata and Ostertag, 2001; Lu et al., 2002) at local and regional scales, as occurs in areas previously degraded by open pit mining. Meanwhile, Feldpausch et al. (2004) recorded a higher accumulation of AB and wood NPP in secondary forests (12-14 years of recovery) of the Amazon in areas with higher edaphic content of total N.

This evidences the strong influence of soil nutrients on the wood NPP of tropical secondary forests, including those generated by mining.

It is important to mention that, although some studies have not shown a significant relationship between soil nutrients and AB accumulation in tropical secondary forests (Poorter et al., 2016; Oberleitner et al., 2021), fertilization experiments developed to evaluate the nutritional limitation of wood NPP in secondary forests, have had different revealing results (Vitousek and Farrington, 1997; Harrington et al., 2001; Davidson et al., 2004). For example, Harrington et al. (2001) reported higher wood NPP with N and P application in secondary forests limited by N (young secondary forest) and P (old secondary forest), respectively. Likewise, Campo and Vázquez-Yanes (2004) observed a greater litter production (NPP component) with the application of N+P in young (10 years) and old (60 years) secondary dry forests, respectively. Similarly, Davidson et al. (2004) recorded a higher wood NPP with the application of N and N+P in six-year-old secondary forests in the Amazon. These experiments show the limitation of N in early successional stages (Davidson et al., 2004) and the restriction of P in late successional stages (Harrington et al., 2001). Likewise, these results show the influence of different soil nutrients on the wood NPP in successional processes, which denotes a multiple nutritional limitation (Kaspari et al., 2008; Sullivan et al., 2014), as could be asserted in the present study.

The fact of registering a higher wood NPP in post-mining forests with high OM and total N contents is similar to that reported in secondary forests of the Amazon, where a higher wood carbon capture was observed in forests with higher total N in the soil (Feldpausch et al., 2004; Kalamandeen et al., 2020). In particular, the fact that wood NPP increases with total N is crucial, because this nutrient is considered one of the limiting factors for plant growth (Lambers et al., 2008a) and NPP of primary tropical forests (Paoli and Curran, 2007; LeBauer and Treseder, 2008; Quinto and Moreno, 2017) and secondary (Feldpausch et al., 2004; Kalamandeen et al., 2020). Total N is fundamental to photosynthesis, formation of ATP and NADPH+ molecules, and in the constitution of chlorophyll (Lambers et al., 2008a); therefore, it is fundamental for the wood NPP of the post-mining forests of the Colombian Pacific. Likewise, the influence of other nutrients (Ca, Mg and ECEC) on the wood NPP, denotes a limitation due to multiple nutrients (Paoli and Curran, 2007; Kaspari et al., 2008), which shows the need to develop active restorations, applying various nutrients in abandoned mines.

A particular aspect observed in the present investigation was wood NPP did not present a significant relationship with the availability of edaphic P in post-mining forests; which is contrary to what has been reported in old secondary forests (Vitousek and Farrington, 1997; Harrington et al., 2001), and in mature tropical forests (Cleveland et al., 2011), such as those of the Amazon (Aragão et al., 2009), Indonesia (Paoli and Curran, 2007) and the biogeographic Chocó (Quinto et al., 2017). Possibly, the little relationship registered between the wood NPP and the P available in post-mining forests is due to reasons such as: 1) the little variation registered in the P available from the post-mining soil, since with mining and the subsequent succession edaphic always presented high values (P available = 26.02 *vs* 32.09 ppm) (Quinto et al., 2022), with which, there was no true deficiency gradient in the soil; 2) the adaptive strategies developed to acquire edaphic P, such as mycorrhizal associations and the growth of a "cluster" network of fine roots that extract the P present in insoluble inorganic phosphates in the soil (Lambers et al., 2008b); with which, the wood NPP rates tend to be similar and make it difficult to show relationships with the P available from the soil.

Could it be that there are limitations of the wood NPP due to the availability of soil nutrients (N and P) in post-mining forests, as suggested by the published hypotheses (Vitousek, 1984; Lambers et al., 2008b; Kalamandeen et al., 2020)?

The hypothesis of nutritional limitation of the wood NPP of the forest has been raised by soil P availability and total N with the succession (Walker and Syers, 1976); according to which, in tropical soils with initial successional ages, there is little availability of N, due to its reduced biological fixation and scarcity of leguminous plants (Walker, 1993; Davidson et al., 2004). However, to the extent that there is a greater colonization of N-fixing plants, the biomass of the ecosystem increases and the succession advances, its availability increases, and this limitation is reduced

(Cleveland et al., 1999; Walker and del Moral, 2008). Whereas, the levels of P in the soil tend to be high in the first successional stages, and over time its availability tends to decrease and be limited in the ecosystem (Vitousek et al., 2010), due to losses by leaching and immobilization in Fe and Al oxides, especially in tropical clayey soils (Walker and Syers, 1976; Vitousek et al., 1993; Reed et al., 2011).

This hypothesis was partially corroborated in the present investigation, given it was observed wood NPP and the total N are positively correlated in post-mining forests; as has been proposed for secondary forests (Vitousek and Farrington, 1997; Harrington et al., 2001; Davidson et al., 2004; Feldpausch et al., 2004); while there was no significant correlation with the available P content. Which is similar to what has been recorded in other investigations (Feldpausch et al., 2004). However, in the post-mining forests, there was also a correlation between the wood NPP and the OM, Ca and Mg contents of the soil; which shows that, in initial stages of the succession, not only can there be a limitation by total N (Kalamandeen et al., 2020), but also, there is a limitation by multiple soil nutrients, in areas previously degraded by mining.

Conclusions

In post-mining forests, soil nutrients determined the wood NPP, and multiple limitations of nutrients with the succession were observed, corroborating the need to restore the degraded ecosystem. The rates of carbon sequestration reported in post-mining forests in the Colombian Pacific denote the degradation of the functioning of the ecosystem generated by mining and reveal its negative influence on the role of these ecosystems in the carbon balance and in mitigating global climate change. The first years of post- mining forest recovery, when less carbon sequestration and greater damage to the ecosystem is evident compared to other anthropic activities such as agriculture and livestock, show the need to develop restoration processes after mining.

Likewise, the fact that post-mining forests present high rates of wood NPP and carbon sequestration after a few decades of deforestation and mining is an opportunity for the development of reforestation programs of forests, which allow the mitigation of global climate change and the conservation of the Colombian Pacific region.

Acknowledgements

This research was financed through the project: Evaluation of the effect of soil fertilization on the net production of the ecosystem in areas degraded by mining, as a strategy to promote carbon capture and the sale of environmental services in the Chocó Biogeographic (CODE 1128 -852-72243), presented by the Technological University of Chocó DLC, National University of Colombia Medellín, University of Valladolid (Spain), John Von Neumann Pacific Environmental Research Institute, and SENA, and approved by the Ministry of Science, Technology and Innovation.

References

Alvarado A, Raigosa J. Nutrición y fertilización forestal en regiones tropicales. Universidad de Costa Rica. San José. Costa Rica: Asociación Costarricense de la Ciencia del Suelo; 2012.

Álvarez E, Duque A, Saldarriaga J, Cabrera K, De las Salas G, del Valle I, Lema A, Moreno F, Orrego S, Rodríguez L. Tree aboveground biomass allometries for carbon stocks estimation in the natural forests of Colombia. Forest Ecol Manag. 2012;267:297-308. https://doi.org/10.1016/j. foreco.2011.12.013

Alves D, Soares JV, Amaral S, Mello E, Almeida S, Silva OF, Silveira A. Biomass of primary and secondary vegetation in Rondonia, Western Brazilian Amazon. Glob Change Biol. 1997;3:451-
61. https://doi.org/10.1046/j.1365-2486.1997.00081.x

Ángel J, Ordoñez M, Olivero J, Echavarría C, Ayala H, Cabrera M. Consideraciones sobre la minería en el departamento del Chocó y recomendaciones para mejorar la gestión. Cali – Colombia: Geopatrimonio - Universidad de Cartagena - IIAP - WWF; 2019. Available from: http:// biblioteca.udea.edu.co:8080/leo/handle/123456789/6278

Aragão LEO, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jiménez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, Anderson LO, Baker TR, Goncalvez PH, Huamán-Ovalle J, Mamani- Solórzano M, Meir P, Monteagudo A, Peñuela MC, Prieto A, Quesada CA, Rozas-Dávila A, Rudas A, Silva Junior JA, Vásquez R. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences. 2009;6:2441-88. https://doi. org/10.5194/bg-6-2759-2009

Austin A, Vitousek P. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia.

1998;113:519-29. https://doi.org/10.1007/s004420050405

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patiño S, Pitman NA, Silva JNM,

Martinez RV. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob Change Biol. 2004;10:545-62. https://doi.org/10.1111/j.1365-2486.2004.00751.x

Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Papale D. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. Science. 2010;329:834-

8. https://doi.org/10.1126/science.1184984

Brown S. Estimating biomass and biomass change of tropical forests: A primer. Rome: FAO;

1997. (Forestry paper, 134).

Campo J, Vázquez-Yanes C. Effects of nutrient limitation on aboveground carbon dynamics during tropical dry forest regeneration in Yucatán, Mexico. Ecosystems. 2004;7:311-9. https:// doi.org/10.1007/s10021-003-0249-2

Chazdon RL, Broadbent EN, Rozendaal DMA, Bongers F, Zambrano AMA, Aide TM, et al. Carbon

sequestration potential of second-growth forest regeneration in the Latin American tropics.

Science Advances. 2016;2:e1501639. https://doi.org/10.1126/sciadv.1501639

Clark DA, Brown S, Kicklighter DW, Chambers JD, Thomlinson JR, Ni J, Holland E. Net primary production in forest: An evaluation and sinthesis of existing field data. Ecol Appl. 2001b;11:371-84. https://doi.org/10.1890/1051-0761(2001)011[0371:NPPITF]2.0.CO;2

Clark DA, Brown S, Kicklighter DW, Chambers JD, Thomlinson JR, Ni J. Measuring net primary production in forest: Concepts and field methods. Ecol Appl. 2001a;11:356-70. https://doi. org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2

Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RW, Hedin LO, Perakis SS, Latty EF, Von Fischer JC, Elseroad A, Wasson, MF. Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. Global Biogeochem Cy. 1999;13:623-45. https://doi. org/10.1029/1999GB900014

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante M, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ, et al. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecol Lett. 2011;14:939-47. https://doi.org/10.1111/j.1461-0248.2011.01658.x

Davidson EA, Carvalho CJR, Vieira ICG, Figueiredo RD, Moutinho P, Ishida FY, Santos MTP, Guerrero JB, Kalif K, Saba RT. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol Appl. 2004;14:150-63. https://doi.org/10.1890/09-0636.1

Del Grosso S, Parton W, Stohlgren T, Zheng DL, Bachelet D, Prince S, Hibbard K, Olson R. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology. 2008;89:2117-26. https://doi.org/10.1890/07-0850.1

Diaz WA, Elcoro S. Plantas colonizadoras en áreas perturbadas por la minería en el Estado Bolívar, Venezuela. Acta Bot Venez. 2009;32:453-66.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J. Carbon pools and flux of global forest ecosystems. Science. 1994;263:185-90. https://doi.org/10.1126/ science.263.5144.185

Environmental Law Alliance Worldwide - ELAW. Guidebook for evaluating mining project EIAs. Eugene, Oregon: ELAW; 2010. Available from: www.elaw.org.

Feldpausch TR, Rondon MA, Fernandes E, Riha SJ, Wandelli E. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecol Appl. 2004;14:S164-76. https://doi.org/10.1890/01-6015

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science. 1998;281:237-40. https://doi. org/10.1126/science.281.5374.237

Forero-Peña LA, Leiva-Rojas EI, Ramírez-Pisco R. Is it possible that the structure of tropical rainforests has recovered 40 years after clear-cutting? For Stud. 2022;76:64-75.

Gentry A. A field guide to the families and genera of woody plants of northwes South América.

Washington, D.C. Conservation International; 1993.

Giljum S, Maus V, Kuschnig N, Luckeneder S, Tost M, Sonter LJ, Bebbington AJ. A pantropical assessment of deforestation caused by industrial mining. PNAS. 2022;19:e2118273119. https:// doi.org/10.1073/pnas.2118273119

Grace J. Understanding and managing the global carbon cycle. J Ecol. 2004;92:189-202. https:// doi.org/10.1111/j.0022-0477.2004.00874.x

Guariguata MR, Ostertag GR. Neotropical secondary forest successions: Changes in structural and functional characteristics. Forest Ecol Manag. 2001;148:185-206. https://doi.org/10.1016/ S0378-1127(00)00535-1

Harrington RA, Fownes JH, Vitousek PM. Production and resource use efficiencies in N and P-limited tropical forests: a comparison of responses to long-term fertilization. Ecosystems. 2001;4:646-57. https://doi.org/10.1007/s10021-001-0034-z

Holl KD. Tropical moist forest. In: Perrow MR, Davy AJ, editors. Handbook of ecological restoration. Vol 2: Restoration in practice. Cambridge: Cambridge University Press; 2002. p. 539-58.

Hoshmand AR. Statistical methods for environmental and agricultural sciences. 2nd ed. Boca Raton: CRC Press; 1998.

Intergovernmental Panel on Climate Change - IPCC. Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the

intergovernmental panel on climate change.Geneva, Switzerland: IPCC; 2014. Available from:

https://www.ipcc.ch/report/ar5/syr/.

Jiménez EM, Moreno FH, Lloyd J, Peñuela MC. Fine root dynamics for forests on contrasting soils in the Colombian Amazon. Biogeosciences. 2009;6:2809-27. https://doi.org/10.5194/bg-6-2809- 2009

Johnson CM, Zarin DJ, Johnson AH. Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology. 2000;81:1395-401. https://doi.org/10.1890/0012- 9658(2000)081[1395:PDABAI]2.0.CO;2

Kalamandeen M, Gloor E, Johnson I, Agard S, Katow M, Vanbrooke A, Ashley D, Batterman SA, Ziv G, Holder-Collins K, Phillips OL, Brondizio ES, Vieira I, Galbraith D. Limited biomass recovery from gold mining in Amazonian forests. J Appl Ecol. 2020;57:1730-40. https://doi. org/10.1111/1365-2664.13669

Kaspari M, Garcia MN, Harms KE, Santana M, Wright SJ, Yavitt JB. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol Letts. 2008;11:35-43. https://doi.org/10.1111/ j.1461-0248.2007.01124.x

Lambers H, Chapin III FS, Pons TL. Plant physiological ecology. 2nd ed. New York: Springer Science; 2008a. https://doi.org/10.1007/978-0-387-78341-3

Lambers H, Raven JA, Shaver GR, Smith SE. Plant nutrient-acquisition strategies change with

soil age. Trends Ecol Evol. 2008b;23:95-103. https://doi.org/10.1016/j.tree.2007.10.008

LeBauer DS, Treseder KK. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology. 2008;89:371-9. https://doi.org/10.1890/06-2057.1

León JD, Osorio NW. Role of litter turnover in soil quality in tropical degraded lands of Colombia. Sci World J. 2014;2014:693981. https://doi.org/10.1155/2014/693981

Linger E, Hogan A, Cao M, Zhang W, Yang X, Hu Y. Precipitation influences on the net primary productivity of a tropical seasonal rainforest in Southwest China: A 9-year case study. Forest Ecol Manag. 2020;467:118153. https://doi.org/10.1016/j.foreco.2020.118153

Lu D, Moran E, Mausel P. Linking Amazonian secondary succession forest growth to soil

properties. Land Degrad Dev. 2002;13:331-43. https://doi.org/10.1002/ldr.516

Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik C, Difiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LM, Monteagudo A, Neill DA, Vargas PN, Patiño S, Pitman NA, Quesada CA, Salomão R, Silva JNM, Lezama AT,

Martínez RV, Terborgh J, Vinceti B, Lloyd J. The above-ground coarse wood productivity of 104 neotropical forest plots. Glob Change Biol. 2004;10:563-91. https://doi.org/10.1111/j.1529- 8817.2003.00778.x

Malhi Y, Doughty C, Galbraith D. The allocation of ecosystem net primary productivity in tropical forests. Phil Trans R Soc B. 2011;366:3225-45. https://doi.org/10.1098/rstb.2011.0062

Maus V, Giljum S, Silva DM, Gutschlhofer J, Rosa RP, Luckeneder S, Gass SLB, Lieber M, McCallum I. An update on global mining land use. Sci Data. 2022;9:433. https://doi.org/10.1038/ s41597-022-01547-4

Moran EF, Brondizio E, Tucker JM, Silva-Fosberg MC, McCracken S, Falesi I. Effects of soil fertility and land-use on forest succession in Amazônia. Forest Ecol Manag. 2000;139:93-108. https:// doi.org/10.1016/S0378-1127(99)00337-0

Oberleitner F, Egger C, Oberdorfer S, Dullinger S, Wanek W, Hietz P. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica.

Forest Ecol Manag. 2021;479:118580. https://doi.org/10.1016/j.foreco.2020.118580

Osorio NW. Manejo de nutrientes en suelos del trópico. Colombia: Editorial L. Vieco S.A.S; 2014.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Hayes DA. Large and persistent carbon sink in the world's forests. Science. 2011;333:988-93. https://doi.org/10.1126/ science.1201609

Paoli G, Curran L. Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo. Ecosystems. 2007;10:503-18. https://doi.org/10.1007/s10021- 007-9042-y

Phillips OL, Malhi Y, Higuchi N, Laurance W, Núñez P, Vásquez M, Laurance S, Ferreira L, Stern M, Brown S, Grace J. Changes in the carbon balance of tropical forest: Evidence from long-term plots. Science. 1998;282:439-42. https://doi.org/10.1126/science.282.5388.439

Poorter L, Bongers F, Aide TM, Almeyda AM, Balvanera P, Becknell JM, et al. Biomass resilience

of Neotropical secondary forests. Nature. 2016;530:211-4. https://doi.org/10.1038/nature16512

Posada JM, Schuur EAG. Relationships among precipitation regime, nutrient availability, and carbon turnover in tropical rain forests. Oecologia. 2011;165:783-95. https://doi.org/10.1007/ s00442-010-1881-0

Poveda IC, Rojas CA, Rudas A, Rangel JO. El Chocó biogeográfico: Ambiente físico. In: Rangel JO. Colombia Diversidad Biótica IV. El Chocó biogeográfico/Costa Pacífica. Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia; 2004. p. 1-21.

Primack RB. A primer of conservation biology. 4th ed. Sunderland: Sinauer Associates Inc; 2008.

Primack RB, Vidal O. Introducción a la biología de la conservación. México: Fondo de Cultura
Económica; 2019.

Quinto H, Ayala-Vivas G, Gutiérrez H. Contenido de nutrientes, acidez y textura del suelo en áreas degradadas por la minería en el Chocó biogeográfico. Rev Acad Colomb Cienc Exacr Fis Nat. 2022;46:514-28. https://doi.org/10.18257/raccefyn.1615

Quinto H, Cuesta-Nagles J, Mosquera-Sánchez I, Palacios-Hinestroza L, Peñaloza H. Biomasa vegetal en zonas degradadas por minería en un bosque pluvial tropical del Chocó
Biogeográfico. Rev Biodivers Neotrop. 2013;3:53-64. https://doi.org/10.18636/bioneotropical. v3i1.127

Quinto H, Mena-Domínguez Y, Valoyes-Hinestroza H. Relación entre la producción de hojarasca y las condiciones edáficas en bosques pluviales tropicales del Chocó Biogeográfico, Colombia. Actual Biol. 2017;39:29-40. https://doi.org/10.17533/udea.acbi.v39n106a03

Quinto H, Moreno F. Net primary productivity and edaphic fertility in two pluvial tropical forests in the Chocó biogeographical region of Colombia. PLoS ONE. 2017;12:e0168211. https://doi. org/10.1371/journal.pone.0168211

Quinto H, Moreno FH. Precipitation effects on soil characteristics in tropical rain forests of the Chocó biogeographical region. Rev Fac Nac Agron Medellín. 2016;69:7813-23. https://doi. org/10.15446/rfna.v69n1.54749

R Development Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2013. Available from: http://www.R-project.org/.

Ramírez G, Quinto H, Vargas-Porras L, Rangel JO. Temporary effect of mining on breathing and on the physicochemical conditions of soil. Mod Environ Sci Eng. 2019;5:837-48. https://doi. org/10.15341/mese(2333-2581)/09.05.2019/007

Ramírez G, Rangel-Ch JO. Sucesión vegetal en áreas de minería a cielo abierto en el bosque pluvial tropical del departamento del Chocó, Colombia. Rev Acad Colomb Cienc Exacr Fis Nat. 2019;43:673-88. https://doi.org/10.18257/raccefyn.896

Rangel JO. Colombia Diversidad Biótica IV. El Chocó biogeográfico/Costa Pacífica. Bogotá:

Instituto de Ciencias Naturales, Universidad Nacional de Colombia; 2004.

Reed SC, Townsend AR, Taylor PG, Cleveland CC. Phosphorus cycling in tropical forests growing on highly weathered soils. In: Bünemann E, Oberson A, Frossard E, editors. Soil Biology - Phosphorus in action. Berlin, Heidelberg: Springer; 2011. https://doi.org/10.1007/978-3-642- 15271-9_14

Sansupa C, Purahong W, Wubet T, Tiansawat P, Pathom-Aree W, Teaumroong N. Soil bacterial communities and their associated functions for forest restoration on a limestone mine in northern Thailand. PLoS ONE. 2021;16:e0248806. https://doi.org/10.1371/journal.pone.0248806

Schuur EA. Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. Ecology. 2003;84:1165-70. https://doi.org/10.1890/0012-9658(2003)084[1165:PA GCRT]2.0.CO;2

Silver WL, Ostertag R, Lugo AE. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor Ecol. 2000;8:394-407. https://doi. org/10.1046/j.1526-100x.2000.80054.x

Sullivan BW, Alvarez-Clare S, Castle SC, Porder S, Reed SC, Schreeg L, Cleveland CC, Townsend AR. Assessing nutrient limitation in complex forested ecosystems: Alternatives to large-scale fertilization experiments. Ecology. 2014;95:668-81. https://doi.org/10.1890/13-0825.1

Tucker JM, Brondizio ES, Moran EF. Rates of forest regrowth in eastern Amazonia: A comparison of Altamira and Bragantina Regions, Parâ State, Brazil. Interciencia. 1998;23:64-73.

Valois-Cuesta H. Sucesión primaria y ecología de la revegetación de selvas degradadas por minería en el Chocó, Colombia: Bases para su restauración ecológica [thesis]. España: Universidad de Valladolid; 2016.

van der Sande MT, Arets EJMM, Peña-Claros M, Hoosbeek MR, Cáceres-Siani Y, van der Hout P, Poorter L. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. Funct Ecol. 2018;32:461-74. https://doi. org/10.1111/1365-2435.12968

Vitousek PM. Litterfall, nutrient cycling and nutrient limitation in tropical forests. Ecology. 1984;65:285-98. https://doi.org/10.2307/1939481

Vitousek P, Porder S, Houlton BZ, Chadwick OA. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl. 2010;20:5-15. https://doi. org/10.1890/08-0127.1

Vitousek PM, Farrington H. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. Biogeochemistry. 1997;37:63-75. https://doi. org/10.1023/A:1005757218475

Vitousek PM, Walker LR, Whiteaker LD, Matson PA. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. Biogeochemistry. 1993;23:197-215. https://doi.org/10.1007/BF00023752

Walker LR. Nitrogen fixers and species replacements in primary succession. In: Miles J, Walton DWH, editors. Primary succession on land. Oxford: Blackwell; 1993. p. 249-72.

Walker LR, del Moral R. Lessons from primary succession for restoration of severely damaged habitats. Appl Veg Sci. 2008;12:55-67. https://doi.org/10.1111/j.1654-109X.2009.01002.x

Walker TW, Syers JK. The fate of phosphorus during pedogenesis. Geoderma. 1976;15:1-19.
https://doi.org/10.1016/0016-7061(76)90066-5

Whitmore TC. An introduction to Tropical Rain Forests. 2nd ed. Oxford: Oxford University Press; 1998.

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Change Biol. 2011;17:927-42. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Zhang J, Tang X, Zhong S, Yin G, Gao Y, He X. Recalcitrant carbon components in glomalin- related soil protein facilitate soil organic carbon preservation in tropical forests. Sci Rep.
2017;7:2391. https://doi.org/10.1038/s41598-017-02486-6

ARTÍCULO 3

Influence of Mining on Nutrient Cycling in the Tropical Rain Forests of the Colombian Pacific.[11]

Abstract.

Nutrient recycling is a fundamental process for the functioning of tropical forests; however, anthropogenic activities such as mining could affect this process in tropical ecosystems. Given that little is known about the effects of mining on nutrient recycling in tropical forests, the objective was set to evaluate the influence of mining on nutrient cycling in tropical rainforests of the Colombian Pacific. Additionally, the hypothesis that nutrient cycling could be lower in post-mining areas was evaluated. To evaluate the effect of mining on nutrient cycling, permanent plots were established in mature and post-mining forests. In both forests, soil acidity, aluminum (Al), organic matter (OM), total nitrogen (N), available phosphorus (P), magnesium (Mg), potassium (K), calcium (Ca), and effective cation exchange capacity (ECEC) were considered. Likewise, the litter production, decomposition, and accumulation on the ground were determined; additionally, nutrient content and nutrient use efficiency (NUE) were determined. It was observed that mining influenced the nutrient contents of the soil in a different way. It was evident that total N and soil OM were similar in both forests, while the contents of P, K, Ca, Mg, Al, and ECEC available were higher in post-mining. The litterfall production and litter mass accumulation on the ground were greater in post-mining, while litter decomposition was greater in mature forests. In mature forests, there was higher foliar content of N, Ca, and B and, in addition, higher NUE of Ca. However, in

[11] Quinto Mosquera, H[11].; Torres-Torres, J.J[11].; Pérez-Abadía, D. (2024)[11]. Influence of Mining on Nutrient Cycling in the Tropical Rain Forests of the Colombian Pacific. ***Forests*** 2024, 15, 1222. https://doi.org/10.3390/f15071222

post-mining, there was higher leaf content of K, Mg, P, Fe, Cu, Mn, and Zn and, in addition, greater NUE of N, P and K. In conclusion, an increase in post-mining nutrient cycling was noted as a strategy for nutrient conservation, and recovery of the functioning and maintenance of productivity in degraded Pacific ecosystems. Consequently, it is expected that in the future, if mining continues in the region, productivity and nutrient recycling will be altered.
Keywords: calcium; litter decomposition; litterfall production; mining; nitrogen; organic matter; phosphorus; potassium; tropical rainforests

Introduction

Tropical forests are considered the most important terrestrial ecosystems in the world [1], due to their high biodiversity [2,3], rates of endemism [4], and carbon sequestration rates [5], and their role in regulating global climate change [6]. In particular, high sequestration rates and carbon balance are determined by environmental factors such as soil type and nutrient content [7,8]. However, most low-altitude tropical rainforests with high net primary productivity (NPP) have infertile, acidic, and nutrient-poor soils [9]. Consequently, this high NPP is influenced and supported by ecological processes of the ecosystem, such as nutrient uptake and cycling [10,11].

Nutrient cycling is a fundamental process for the functioning of tropical forests [11,12], which includes the weathering of rocks, the release of nutrients into the soil solution, mineral leaching, nutrient absorption, translocation of nutrients within plants, herbivory, leaf litterfall, and, finally, the decomposition of organic matter (OM) from the soil [9,11,13]. In summary, nutrient cycling includes the processes of utilization and reuse of mineral nutrients between soil and plants [10,12]. Consequently, environmental and biological factors that regulate nutrient storage processes in the soil, and the litter production and decomposition, also directly determine nutrient cycling [10,14]. For example, Austin and Vitousek [15] and Quinto and Moreno [16] reported that soil nutrient contents tend to decrease with increasing annual precipitation levels.

On the other hand, Walker and Syers [17], Guariguata and Ostertag [18], Davidson et al. [19], Walker and del Moral [20], Dalling et al. [21], and Quinto et al. [22] denoted that the contents of nutrients such as P, N, Ca, and Mg change with succession time. In particular, it was observed that the contents of available P tend to decrease until it is a limiting factor [17,21,23]; however, N contents tend to increase over time [19,20,24]. For example, studies carried out by Li et al. [25] show that pH, NH_4+, P, and K concentrations decrease with succession, while Quinto et al. [22] denoted a change in the contents of P, total N, Ca, K, and OM with succession in forests. This shows the influence of succession age on nutrient content [19].

In synthesis, soil nutrient content is determined by the interaction of soil factors, such as climate [15,16], organisms (solubilizing bacteria of P and N fixers) [26], topog- raphy, parental material, time (succession) [17,19,25], and land use [10,18,22,27]. Conse- quently, the magnitude of nutrient content is determined by the action of these factors [28]. For its part, litterfall production is determined by factors such as precipitation [29,30], plant species, age of the forest, successional stage, topography, temperature, and edaphic conditions [31,32]. Nutrient content and soil type are the main drivers of such production in tropical forests [8,32,33]. Particularly, the content of P, N, Ca, Mg, K, and OM in the soil generates greater litterfall production [7,34], and especially, the contents of N, P, and K tend to be the most limiting [33,35–37]. Likewise, different research shows that as well as litterfall production, the foliar nutrient content is related to soil nutrient content in forests [12,21,33,38,39].

For its part, litter decomposition, a fundamental process of nutrient recycling, is determined by factors such as the physical and climatic environment (temperature and hu- midity), the decomposing microbial community, the quantity and quality of the OM [40–43], soil properties [44], oxygen availability [45,46], nutrient content, cellulose, lignin, ratio C:N, plant species [41,47–49], and type of vegetation cover [50,51]. In particular, soil nutrient content is an important factor controlling decomposition because it influences the activity of decomposers, thereby considerably promoting decomposition [43,52–54]. Consequently, any affectation of the vegetation, and/or the nutrient contents of the soil, can affect litter production and decomposition, and with it, the nutrients cycling of the ecosystem [10,19,48].

In tropical forests, despite the complexity that the nutrient cycling process denotes, since many environmental and biological factors affect each of the processes [11,12,55], it is essential to understand how anthropic disturbances such as deforestation, forest degradation, livestock farming, and open pit mining [27,56] influence the nutrients cycling and recycling [19], even more so if the importance of these processes for the functioning of the ecosystem is considered. In this sense, it has been shown that in recent decades open pit mining has generated the destruction of about 1680 km^2 of natural forests in tropical regions [3,56]. In addition, mining destroys soil horizons [57], reduces vegetation [58], and affects biodiversity [59]; consequently, it possibly alters ecosystem functioning, including nutrient cycling [60].

Specifically, in the Colombian Pacific, mining has generated the degradation of more than 360 hectares of forest annually [59], and, until 2015, licenses had been granted for the exploitation of more than 300 thousand hectares of natural forest, which represents 6.49% of the territory [61]. This shows the impact on the vegetation and soil nutrients of the ecosystem [22]. However, little is known about the effects of mining on ecosystem nutrient cycling in tropical rainforests [60]. Based on the above, the objective was set to evaluate the influence of mining on nutrient cycling in the tropical rainforests of the Colombian Pacific.

Materials and Methods

Study Area

The present study was carried out between 2019 and 2022, in forested areas previously degraded by open-pit gold mining in the town of Jigualito (5 06 01 N–76 32 44 W), and the mature tropical rain forests of Opogodó (municipality of Condoto) in the state of Chocó, Colombia. These forests (mature and post-mining) were located less than five kilometersapart; therefore, they presented similar levels of precipitation, altitude, and temperature, which have an average rainfall of 8000 mm per year, and a mean temperature is 26 C, an altitude of 70 m and flat topography. This locality is part of the North Central Chocó biogeographical region, which includes the upper basins of the Atrato and San Juan rivers, in Piedemonte and Colinas low landscape units with humid terraced soils and with a type of transitional sedimentary rock [62]. The localities are within the geomorphological unit of the Sedimentary Hills of the Tertiary period, which are formed by sedimentary rocks of low altitude, composed of sandy claystone, sandstone, and limestone. The forests are mostly primary, mature, and secondary with different ages of recovery after the impact of mining has been carried out in the area at different times.

In the mature forest, the most abundant tree species were *Wettinia quinaria*, *Mabea occidentalis*, *Eschweilera sclerophylla, Vismia* sp., *Inga* sp., *Pourouma chocoana*, *Vismia macro- phylla*, *Matisia* sp., *Protium apiculatum*, *Couepia platycalyx*, *Miconia* sp., *Sloanea grandiflora*, *Sloanea fragrans*, *Anaxagorea crassipetala*, *Humiriastrum melanocarpum*, *Faramea jefensis*, *Ces- pedesia spathulata*, *Chrysochlamys clusiifolia*, and *Brosimum utile* [63,64], while in post-mining forests, the most dominant tree species were *Cecropia peltata*, *Vismia baccifera*, *Cosmibuena macrocarpa*, *Ochroma pyramidalis*, *Welfia regia*, *Pityrogramma calomelanos*, *Cespedesia spathulata*, *Perebea xanthochyma*, *Inga chocoensis*, *Pourouma bicolor*, and *Ocotea cernua* [65]. In these forests, aboveground biomass of 35.17 t ha^{-1} and 178.32 t ha^{-1} was recorded at 30–35 years and mature forest, respectively [66], while a wood net primary productivity of between

6.25 t ha^{-1} year^{-1} and 9.8 t ha^{-1} year^{-1} was recorded at 30–35 years and mature forest, respectively [66]. In post-mining forests of 30–35 years, the fine root biomass was lower, with average values of 2.56 t ha^{-1}. But, in mature forests, the fine root biomass was

5.91 t ha^{-1} [67].

The soils of post-mining forests are ultisols, but due to mining, they are characterized by a lot of rocky material and sand. In addition, they are acidic and have high contents of OM (13.9%), total N (0.58%), available P (32.0 mg kg^{-1}), Al (2.7 $cmol_c$ kg^{-1}), and clay, while the concentrations of Ca (5.8 $cmol_c$ kg^{-1}), K (0.36 $cmol_c$ kg^{-1}), Mg (2.5 $cmol_c$ kg^{-1}), ECEC (11.5 $cmol_c$ kg^{-1}) and silt are very low in areas of recent mining activity, but their content is higher in areas with more recovery time [22]. On the other hand, the soils of the

mature forests surrounding the mines present extreme acidity, with high contents of Al (0.12 $cmol_c$ kg^{-1}), OM (11.9%) and total N (0.6%), and low amounts of P (1.3 mg kg^{-1}), Mg (0.2 $cmol_c$ kg^{-1}) and Ca (0.38 $cmol_c$ kg^{-1}), while the K (0.2 $cmol_c$ kg^{-1}) contents are intermediate and ECEC (1.0 $cmol_c$ kg^{-1}) is low [16].

Methods

Experimental Design

A design stratified by age of succession was used, with two strata for sampling. Stratum 1 corresponded to areas that had a recovery time of 30–35 years post-mining. In this, tree vegetation with greater diameter and species richness was found. Stratum 2 corresponded to primary forests present in the region and was taken as the reference scenario. In mature forests, the blocks consisted of 37 random permanent plots of 10 × 10 m (100 m^2). In post-mining forests, 125 random permanent plots of 10 × 10 m (100 m^2) were established.

Measurement of Physical and Chemical Parameters of Soil

In each plot (37 and 125 in post-mining and mature forest, respectively), composite samples of soil were taken at a depth of 20 cm, to which the parameters of acidity (pH), Al, OM, total N, available P, Ca, K, Mg, ECEC, and texture (percentages of sand, silt, and clay), according to the following laboratory techniques: Bouyoucos for textural fractions, poten- tiometric in water solution (1:2) for pH, Walkley and Black with the respective coefficient to determine OM, Micro-Kjeldahl for total N, ascorbic acid in an UV-VIS spectrophotometer after extraction with the Bray II method for available P, atomic absorption for Ca, Mg, and K extracted with ammonium acetate, described in Quinto et al. [22]. Soil sampling was carried out in the years 2020 and 2021.

Measurement of the Litterfall Production

The litterfall production was determined with litter collectors (75 in mature forests, and 60 in post-mining) of 1.0 m × 0.5 m of the area of collection for a year [31]; these litter collectors were distributed according to the established treatments. The collected material was dried and weighed; this material was not separated, and the total values stored in each collector were taken biweekly. The quantities collected were expressed in tons per hectare per year (t ha^{-1} year^{-1}) [31].

Measurement of Litter Decomposition

To measure this variable, the decomposition bag method was used, which has been used in different previous studies [47,51,68,69]; for this, initially, the leaves of the dominant tree species in the post-mining and primary forests were collected. The selected leaves were the recently fallen ones that were yellow and without signs of decomposition. Said collected material was taken to the Botany and Ecology Laboratory of Universidad Tecnológica de Chocó, where it was dried in ovens for 48 h until it reached a constant dry weight.

Then, 100 g of dry-weight leaf litter was introduced into each decomposition bag, and, subsequently, the material was taken to each forest from which it was collected, following what was indicated in the experimental design. Subsequently, for 32 days, each week, 10 bags of decomposition were randomly collected, which were taken to the laboratory, and there they were dried and weighed again, and with this information, the quantity of dry weight lost was determined. Using the weight loss data over time, the percentage of remaining mass, the percentage of weight loss, and the decomposition rate (k) were determined in each of the established strata or treatments.

Litter Decomposition Equations

The decomposition rate (k) of litter was determined with the simple exponential model [46,70] of the form as follows:

(1) $$Ln(X0/X1) = k \times T;$$

(2) $$k = Ln(X0/X1)/T.$$

Where Ln is the natural logarithm, k is the decomposition rate in years, X0 is the initial mass (dry weight of the litter), X1 is the mass (dry weight of the litter) remaining at time T, and T is the time in years [9,12,70].

Measurement of the Litter Mass Accumulation on the Ground

The soil litter was determined with the Olson [70] model based on the production and decomposition values of litter of each ecosystem evaluated, in the following way:

Litter mass accumulation = Litterfall production/k

Where k is the decomposition rate in years determined in each of the plots established in mature and post-mining forests. The litter mass accumulation reflects the relationship between litterfall and decomposition [9,10]. Litter mass accumulation on the ground values were presented in tons per hectare (t ha^{-1}).

Measurement of Leaf Nutrient Content

In each plot (37 and 125 in post-mining and mature forest, respectively), composite samples of leaf were taken at a litterfall in the collectors, the collected material was dried and weighed (1.5 kg), to which the parameters of

N, P, Ca, K, and Mg, according to the laboratory techniques, were as follows: Micro-Kjeldahl for total N, ascorbic acid in an UV-VIS spectrophotometer after extraction with the Bray II method for available P, and atomic absorption for Ca, Mg, and K extracted with ammonium acetate, described in Osorio [71]. Foliar sampling was carried out in the years 2020 and 2021.

Determination of Nutrient Use Efficiency (NUE)

To determine the NUE, the Vitousek [33] model was used, through the following equation: NUE = Leaf nutrient content × litterfall production(1)
The NUE was determined for N, P, Ca, and K nutrients in mature and post-miningforests. High NUE values indicate high nutrient use efficiency due to high litter production or high foliar availability of nutrients, while low NUE values indicate the opposite, with oligotrophic conditions in the ecosystem [12,33].

Data Analysis

To evaluate the influence of mining on the physicochemical parameters (acidity, Al, MO, total N, available P, Mg, K, Ca, and ECEC) of the soil, litter production, decompo- sition of litter, litter on the ground, litter nutrient content, and NUE, the non-parametric Mann–Whitney (MW) test was used when the assumptions of normality and homogeneity of data variances and its residuals were not met, and evaluated with the statistical tests of Shapiro–Wilk, Bartlett, Hartley, and Kurtosis (between +2.0 and −2.0), while, when the assumptions were met, the T-Student Test was used. All statistical analyses were performed in the Rstudio version 3.0.0 [72].

Results

Soil Nutrient Content

Mining had a different influence on soil nutrient content in the forests of the Colom- bian Pacific (Figure 1). In this sense, it was observed that the total soil

N was, on average, (±standard error) 0.61 ± 0.02% in mature forests and 0.57 ± 0.04% in post-mining, and it was noted that there were no significant differences between the two forests (MW = −1.24; *p*-value = 0.214) (Figure 1A) hile the available P was 1.32 ± 0.06 ppm in mature forests and 29.52 ± 3.8 ppm in post-mining and a statistically significant difference was noted between the forests (MW = −7.17; *p*-value = 0.00007) (Figure 1B). Likewise, soil K was 0.23 ± 0.01 meq/100 g in mature forests and 0.36 ± 0.02 meq/100 g in post-mining forests, and it was noted that there were significant differences between the forests (MW = −5.43; *p*-value = 0.00005) (Figure 1C). In addition, soil Ca was significantly higher in post- mining forests with 5.8 ± 0.81 meq/100 g, compared to the content of mature forests of 0.38 ± 0.02 meq/100 g (MW = −8.5; *p*-value = 0.00001) (Figure 1D). Also, Mg and ECEC contents were significantly higher in post-mining forests (Figure 1E). For its part, the Al con- tent of the soil was 0.127 ± 0.006 meq/100 g in mature forests and 2.78 ± 0.21 meq/100 g in post-mining, and it was confirmed that there were significant differences between the forests (MW = −9.15; *p*-value = 0.00005).

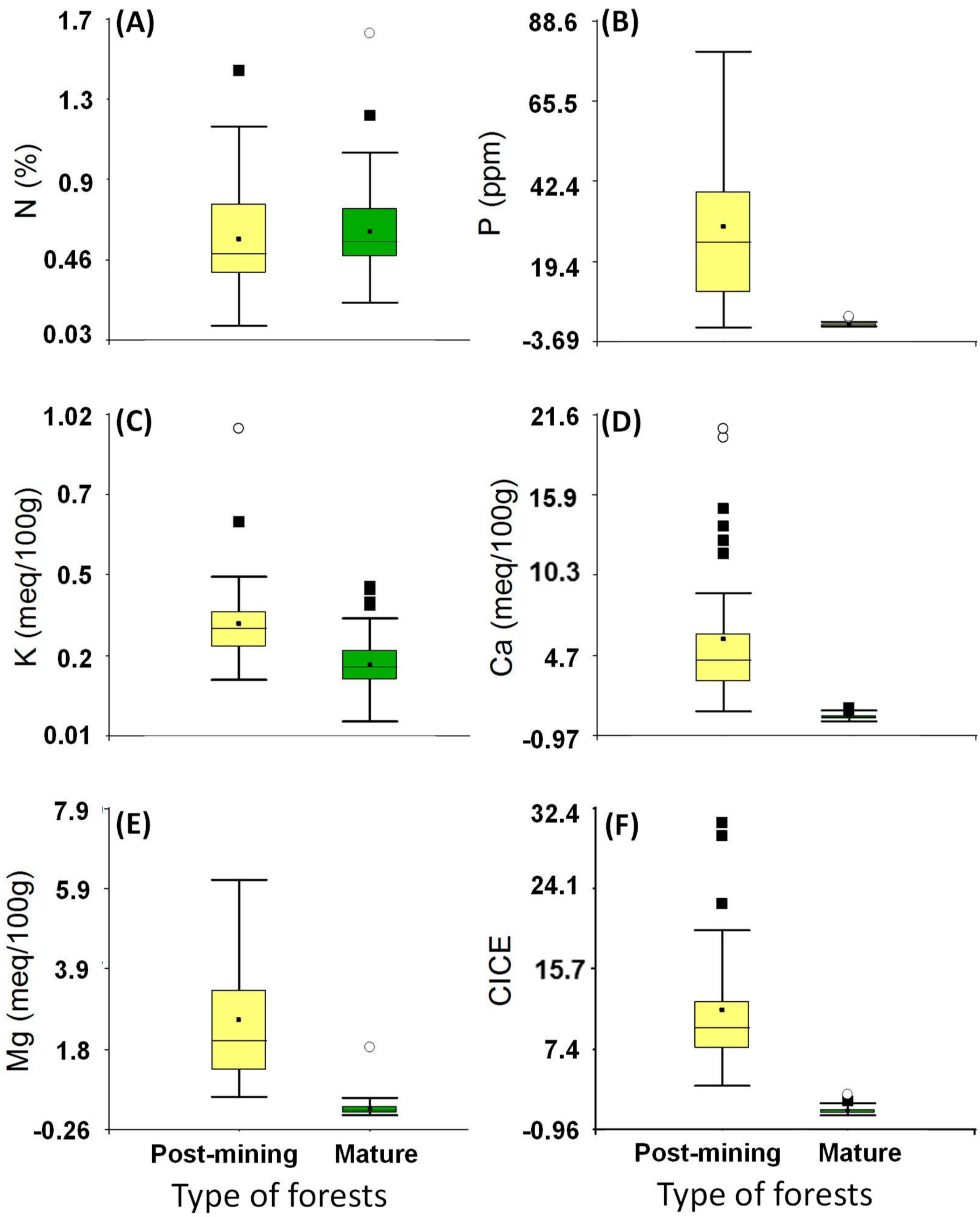

FIgura 5 Effects of mining on soil nutrient content in rainforests of the Colombian Pacific

*(**A**) nitrogen content—N, (**B**) phosphorus content—P, (C) potassium content—K, (**D**) calcium content—Ca, (**E**) magnesium content—Mg, and (**F**) cation exchange capacity—CECC. Post-mining: post-mining forest and Mature: mature forest without significant anthropogenic intervention.*

Litter Dynamics

Litterfall production was 4.29 ± 0.24 t ha^{-1} $year^{-1}$ in mature forests and 9.67 ±0.28 t ha^{-1} $year^{-1}$ in post-mining forests, and significant differences were evident between forest types (T-student = 14.41; *p* < value= 0.000001) (Figure 2A), while the litter decomposi- tion rate was higher in mature forests (k = 6.71 ± 1.43 $year^{-1}$) compared to that recorded in post-mining (k = 2.08 ± 0.5 $year^{-1}$) (MW = −4.5; *p*-value = 0.00006) (Figure 2B). Conse- quently, litter mass accumulation was lower in mature forests (0.63 ± 0.03 t ha^{-1}) compared to that of post-mining forests (4.62 ± 0.13 t ha^{-1}) (T-Student = 27.6; *p*-value < 0.00001) (Figure 2C). Contrary to this, it was observed that the OM was 11.94 ± 0.4% in mature forests and 13.9 ± 1.24% in post-mining, and it was noted that there were no significant differences between the forests (MW = −0.31; *p*-value = 0.75) (Figure 2D).

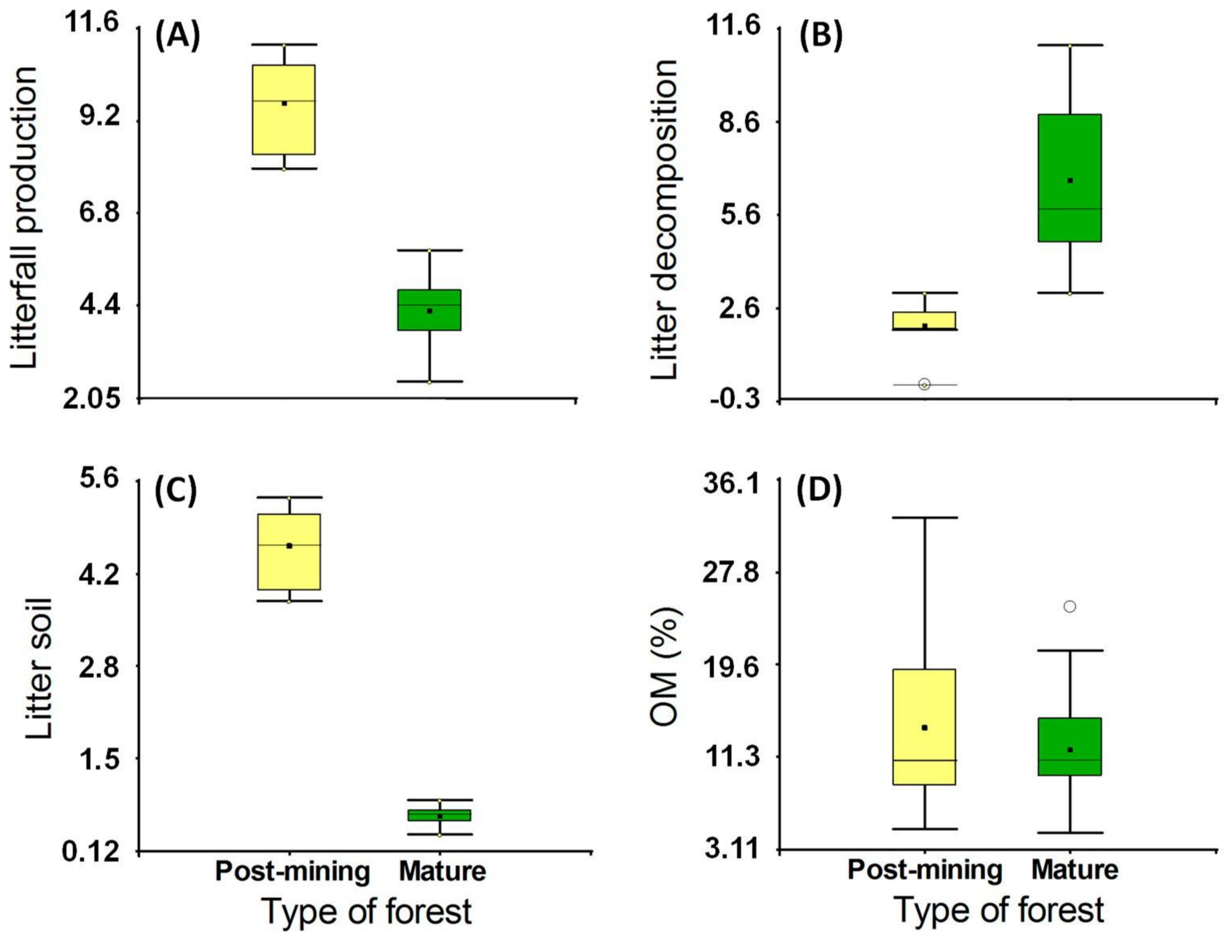

FIgura 6 Effects of mining

(**A**) litterfall, (**B**) litter decomposition, (**C**) litter mass on the ground, and (**D**) organic matter in tropical rain forests of the Colombian Pacific. Post-mining: post-mining forest and Mature: mature forest without significant anthropogenic intervention.

Leaf Nutrient Content

It was determined that in mature forests there was a higher leaf content of N and Ca, respectively (Figure 3A,D), while in post-mining forests there were higher foliar contents of nutrients such as K, Mg, P, and Fe (Figure 3B,C,E,F). For its part, the foliar content of micronutrients such as B was higher in mature forests (Figure

4A); however, foliar contents of Cu, Mn, and Zn were higher in post-mining forests (Figure 4B–D

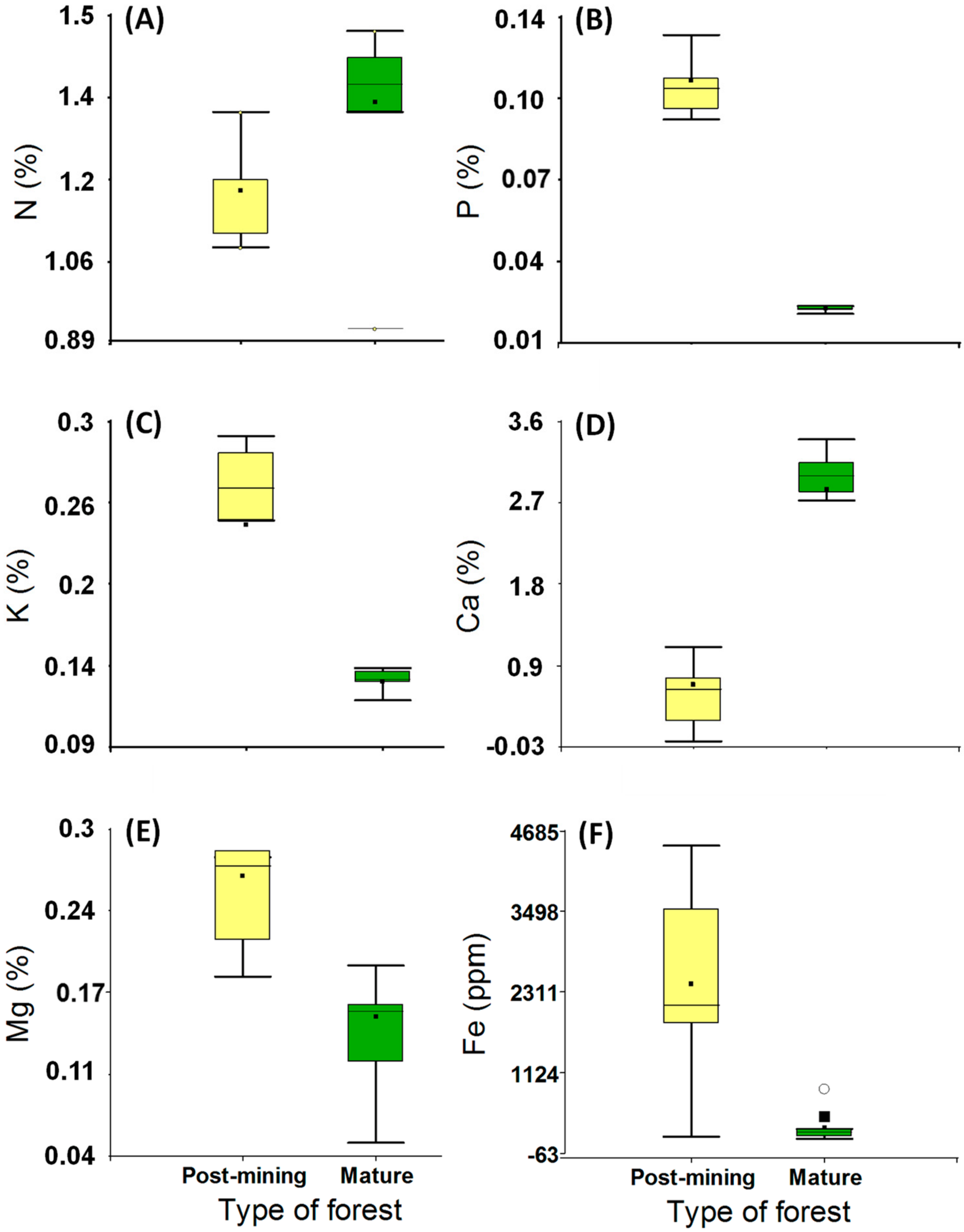

FIgura 7 Effects of mining on foliar nutrients in tropical rain forests of the Colombian Pacific

(**A**) nitrogen content—N, (**B**) phosphorus content—P, (**C**) potassium content—K, (**D**) calcium content—Ca, (**E**) magnesium content—Mg, and (**F**) Iron content—Fe. Post-mining: post-mining forest and Mature: mature forest without significant anthropogenic intervention.

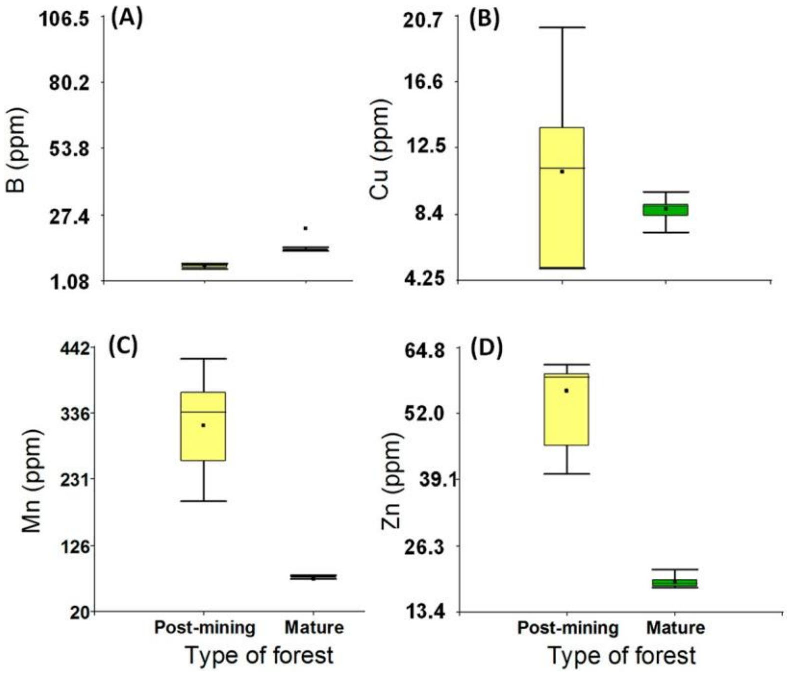

FIgura 8 Effects of mining on foliar nutrients in tropical rain forests of the Colombian Pacific

(**A**) boron content—B, (**B**) copper content—Cu, (**C**) manganese content—Mn, and (**D**) zinc content—Zn. Post-mining: post-mining forest and Mature: mature forest without significant anthropogenic intervention.

Nutrient Use Efficiency (NUE)

It was determined that in post-mining forests there was a greater NUE of N, P, and K (Figure 5A–C), while in mature forests, there was a greater NUE of Ca (Figure 5D).

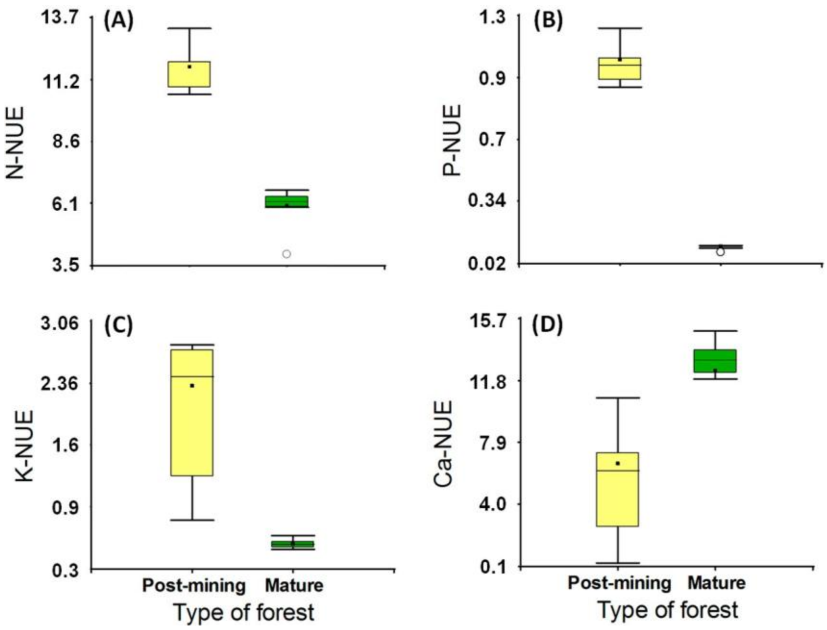

FIgura 9 Effects of mining on nutrient use efficiency (NUE) in tropycal rain forests of the Colombian Pacific

(A) nitrogen use efficiency—N, (B) phosphorus use efficiency—P, (C) potassium use efficiency—K, and (D) calcium use efficiency—Ca. Post-mining: post-mining forest and Mature: mature forest without significant anthropogenic intervention

Discussion

Influence of Mining on Soil Nutrient Content

In the rainforests of the Colombian Pacific, open pit mining generated a significant increase in the contents of soil nutrients such as P, K, Ca, Mg, and ECEC. This increase is probably due to the fact that with the semi-mechanized mining (with backhoes) that is carried out in the region [57,73], the forests are deforested, the organic soil is destroyed, the organic and inorganic horizons of the soil are altered, and the density, texture, and aggregates of the soil are affected due to the mechanical action of the machines [22,57,58]; likewise, the ecosystem is contaminated and biodiversity is lost [59,73]. In addition, due to mining, soil rocks are affected and degraded [73], thereby releasing nutrients that remain available in the soil solution [22]. In short, mining accelerates the release of nutrients resulting from the weathering of rocks.

In this sense, Jordan [10] determined that the cycling, dynamics, and availability of soil nutrients can be influenced by environmental factors such as temperature, humidity (precipitation), productivity, and decomposition, among others, as well as by anthropic fac- tors such as the type, size, and intensity of disturbances that affect an ecosystem [10,18,19]. Consequently, it has been noted that after disturbances such as deforestation, burning of forests, and changes in land use (livestock and crops), among others, there was an increase in the contents of Ca, N, Mg, K, and available P in the soil during the early years [10,19], similar to what was reported in areas degraded by open pit mining [22]. Also, similar to what was reported by Guariguata and Ostertag [19] in an analysis carried out at the level of tropical forests that noted that after deforestation, changes occur in the soil such as increases in the availability of nutrients such as P, Ca, K, Al, and ECEC [19]. These increases are due to the fact that the nutrients that were stored in the plant biomass (leaves, stems, branches, and roots) become available in the soil solution after deforestation and decomposition of the material [10,11]. In summary, the availability of nutrients present in post-mining areas is due to the residues of deforested trees and the minerals released by the mechanical action of mining on the ground.

It is important to mention that not all nutrients increase their availability with mining. For example, total soil N presented similar values in mature forests and post-mining, which indicates that the availability of this nutrient was not affected in principle by deforestation and the impact of the ecosystem by mining [22]. Although a decrease in total N was expected in post-mining areas, its content in the soil was similar to that recorded in mature forests, which is probably due to the interaction and influence of different factors, among which we can mention the following: (1) the presence and abundance of plant species with the capacity to symbiotically fix atmospheric N, of which more than 70 individuals have been recorded, in trees of the Fabaceae family (legumes) in the evaluated post-mining forests (*Inga chocoensis*, *Inga lopadadenia*, *Abarema barbouriana*, *Lonchocarpus monilis*, *Calliandra laxa*, *Diplotropis* sp., *Pentaclethra macroloba*) [74]; (2) the colonization of bacteria (free and symbiotic) fixing atmospheric N, since, if conditions allow, after >30 years of succession, these biological groups can begin to colonize, and thereby increase the rates of nitrification, ammonification, and N fixation in the ecosystem [8,19,22,54,55]; and (3) the presence of total N product of plant biomass and plant residues of trees, bushes, and herbs [14,19] that remained after mining and that are in decomposition and mineralization deposited in the soil, and that would also explain the similarity in availability of N in both forest ecosystems studied.

The high precipitation that occurs in the Colombian Pacific region can favor the leaching of nutrients from the soil [15,16,42], as long as the topography and inclination of the land allow it [14], because in some places in post-mining areas, the miners left holes, gaps, channels, mounds of earth, and concave topographies of the terrain [57,58], in which a large amount of OM accumulates water and minerals; despite the high rainfall, this condition would also explain the high accumulation of nutrients in the post-mining soil.

With open pit mining in soils of the Colombian Pacific, the amount of Al increased and the strong acidity of the soil was maintained [22], which is possibly due to the influence of high precipitation and rocky and clay minerals in the soil [12,71]. Specifically, high precipitation and temperature generate greater acidity of the soil, and also the accumulation of Al in the soil, due to the increase in the weathering of aluminosilicate minerals based on the reactions of hydrolysis, dissolution, carbonation, oxidation, reduction, and hydration, which generate as products the disintegration of the structure of rocks and minerals, and the release of Al and other elements to the soil [12,71].

With precipitation and rock weathering, mineral losses through leaching increase due to its solubility [15]; however, Al can remain in the soil in different forms, such as the following: (1) soluble in the soil solution; (2) exchangeable retained on the surface of negatively charged clays; (3) complexed (fixed) in the soil OM; and (4) precipitated as a secondary mineral as oxide and hydroxide and, as such, remain on the ground [71]. These characteristics would explain the greater accumulation of Al in post-mining soils, where the mechanical action of backhoe machines degraded rocks containing Al in the soil, increasing its availability. However, this increase in the availability of Al in post-mining areas will surely generate toxicity for most of the plants that colonize these degraded areas since the Al saturation is greater than 23.4%, which indicates possible toxicity for most plants [12,71]. This edaphic condition can be a significant problem for the recovery of the ecosystem, because Al toxicity affects the absorption of nutrients, generates chlorosis and necrosis, decreases the size of the leaves, alters metabolic processes, increases nutritional stress, alters physiological processes, affects the development of roots, stems and leaves, reduces the photosynthetic rate and growth of plants, and decreases the biomass and primary productivity of the ecosystem [12,71,75,76]. In summary, despite the release of nutrients that occurs in mines due to the degradation of minerals, the presence of Al, with its respective toxicity, could be a predominant limiting factor that can affect the growth and recovery of biomass and biodiversity of these degraded ecosystems.

In the mature forests of the Colombian Pacific, infertility and the low nutrient content of the region's soils were evident, which agrees with what was stated by Jordan [10], Vitousek and Sanford [77], Whitmore [9], Metcalfe et al. [13], Alvarado [12], and Quinto and Moreno [16], who consider that the majority of tropical rainforests, including those of Chocó, have acidic, weathered, infertile, and nutrient-poor soils. In this sense, Jordan [10] concluded that in poor and infertile (oligotrophic) tropical ecosystems, plants develop nutrient conservation mechanisms, among which we can mention strategies such as the following: (1) The production of greater biomass of fine roots in soils poor in nutrients, as has been previously evidenced [77] and as has been evaluated in Chocó forests [67]. This mechanism occurs because, with a great system of fine roots, more nutrients can be acquired from the soil [55]. (2) The greater concentration of fine roots on the soil surface to acquire more nutrients [78]. (3) The formation of associations with mycorrhizal fungi to increase the absorption of nutrients in conditions of low availability [55,79]. (4) The relocation of nutrients from old leaves to other plant structures before their abscission [13,19,77], where there is greater mobility of nutrients such as P, N, and K. [12,80]. (5) The storage of nutrients in plant biomass [13,19,38]. In this sense, it has been observed that in tropical very rainy forests, there is (>2000 mm annually) greater storage of nutrients in leaves, compared to stems; likewise, it has been noted that Ca and K are stored more in the aboveground biomass than in the soil surface (20 cm deep), while N and P contents tend to be higher in the soil [10]. These nutrient conservation mechanisms are possibly those that the mature rainforests of the Colombian Pacific are using to maintain their nutritional status and cycling, and therefore their primary productivity.

Influence of Mining on Litter Dynamics

In the rain forests of the Pacific, litterfall production was greater in post-mining sec- ondary forests. This trend is probably due to the greater availability of nutrients such as available P, K, Ca, and Mg present in the soil previously degraded by open pit mining. This corroborates what was reported a few decades ago by Jordan [10] and Vitousek and Sanford [77], who concluded that tropical forests with fertile soils and higher nutrient content have greater litterfall production [10,77]. Some years ago, Paoli and Curran [7] reported greater litterfall production in soils with higher nutrient content (K, Ca, Mg, avail- able P, total N, and ECEC) in Lowland Forest at Gunung Palung National Park, in Borneo, Indonesia. Also, Montagnini and Jordan [11] concluded that tropical forests with more fertile soils and/or with greater availability of nutrients have greater litterfall production. Recently, in forests of the Colombian Pacific, a significant relationship between litterfall production and soil nutrient content was noted [34]. Due to the observed correlations and fertilization experiments carried out in different tropical forests, soil N, P, and K have been considered as limiting elements of forest productivity [33,35–37].

In terms of ecosystems degraded by mining, this greater litterfall production is a posi- tive factor for their recovery [48,60], since the litter production and decomposition are the main processes of nutrient cycling [10,12,41], and, consequently, soils with higher nutrient content have greater litterfall production and, respectively, greater nutrient cycling [11]. This high litterfall production seems to be the main mechanism to maintain the proper functioning of eutrophic forests, where there is a high availability of nutrients in the soil compared to oligotrophic forests where litterfall production is usually lower, but the aboveground biomass of trees is greater [81], as reported by Jordan [10] in tropical forests of Sarawak with similar climatic conditions and differences in soil fertility, as was also corroborated in the present study, where post-mining areas with nutrient-rich soils and lower aboveground biomass presented greater litterfall production, and mature forests with infertile soils and greater aboveground biomass presented lower litterfall produc- tion. In summary, it is evident that in ecosystems in oligotrophic conditions and nutrient shortages, there is greater aboveground biomass and more nutrients are stored in the plant biomass, while in eutrophic conditions, it produces more litterfall and greater circulation of nutrients [11,12,77,81]. Likewise, after mining in the forests of the Colombian Pacific, nutrients in the soil increase, and aboveground biomass decreases, but leaf litter production increases; consequently, nutrient cycling increases.

Litter decomposition rates in post-mining and mature rain forests were 2.08 and 6.71 year^{-1}, respectively; these decomposition rates can be considered to be very high, according to the analyses carried out for tropical rainforests [70]. In addition, they are higher than most rates reported for areas of mining in rehabilitation (0.36–0.70 year^{-1}) [60], and in tropical forests between 0.52 and 3.42 year^{-1} [9,10]. Different studies have quantified high rates of OM decomposition in tropical ecosystems with high levels of precipitation [15,43,60] and greater fertility [10,82]. In particular, the nutrient content of the soil is an important factor that controls decomposition because it influences the activity of decomposers (microorgan- isms, fungi, and arthropods, among others), and thus decomposition is favored [43,52–54]. However, the results of the present study are contrary to this hypothesis, since the decom- position rates recorded in nutrient-poor mature forests (oligotrophic) were higher than those recorded in post-mining secondary forests rich in nutrients (eutrophic), with both ecosystems with high levels of average annual precipitation (>8000 mm) (Figure 1). That is, there was greater decomposition in nutrient-poor soils.

The lower litter decomposition recorded in post-mining secondary rainforests is surely due to the differences in the characteristics of the litter of each type of forest since in each type of forest there was a different composition of tree species [58,65,74], which generates differences in the chemical characteristics of the litter because each species has a different foliar nutrient content [10,12,41,55,77]. Specifically, it was observed that in mature forests there was a higher foliar content of N and Ca (Figure 4), which possibly explains the higher decomposition rate of this forest. This assertion is corroborated by what was stated by Hobbie [82], who noted that high foliar contents of N and Ca were associated with rapid rates of leaf litter decomposition. Also, this assertion is supported by the approaches of Montagnini and Jordan [11], who consider that a greater foliar content of nutrients, especially N, favors the decomposition of leaf litter and MO due to the high demand by decomposer organisms [82]. This situation possibly explains the difference in decomposition rates among ecosystems. Furthermore, it is shown that under high precipitation conditions, species composition and foliar nutrient content (Ca and N) can be the best predictors of litter decomposition.

The lower rate of litter decomposition in post-mining forests surely occurs due to nutrient relocation processes prior to leaf abscission in post-mining trees, as a nutrient conservation mechanism [10]; given that, high nutrient contents were recorded in the post- mining soil, but with a decrease in its foliar contents, especially N and Ca. This relocation of nutrients is a common strategy in tropical ecosystems, since it has been recorded in different proportions in tropical forests with moderately fertile and infertile soils [77]. Therefore, low decomposition generates an accumulation of "low-quality" litter (with low N and Ca content) in post-mining soils. The slow decomposition could also be explained by the high precipitation in the region, which generates low-quality litter, similar to what has been previously reported in tropical rainforests [15,45], and also, in forests of biogeographical Chocó [46].

Consequently, the fact of presenting low litter decomposition is a positive characteristic for the natural recovery of soil degraded by mining activity since, due to the slowness of the decomposition process, leaf litter and OM accumulate in the soil, and with this the OM content, percentage of humidity, microbial biomass, nutrient content, macroaggregates, microaggregates, and texture, among others [19,48,71]. In fact, one of the mechanisms used to restore degraded ecosystems includes the application of organic fertilizers [12,58], which in this case occur naturally in post-mining secondary forests after >30 years of succession in the Colombian Pacific.

Given the little litter decomposition in post-mining forests, a litter mass accumulation on the ground forest was noted; said accumulation was 4.62 t ha^{-1}, which is within the range of 1.9 and 11.3 t ha^{-1} recorded for tropical forests [9,10] (Table S1). In this sense, the present values of litter mass on the ground, as well as what is recorded in various studies
carried out in tropical forests, show that a high litterfall production accompanied by low rates of litter decomposition generates an accumulation of litter mass in the soil [9]. In conclusion, this accumulation of litter mass as a result of reduced decomposition shows retention of nutrients in the litter, which restricts its availability for microorganisms and plants, and with this, a slow release of nutrients and a considerable obstruction to nutrient recycling is generated, which could affect the functioning of the post-mining ecosystem. However, if this special condition were not present, the fine leaf litter would decompose and mineralize rapidly, as occurs in mature forests and other

regions of the Chocó bio- geographic region [46], due to high precipitation that facilitates leaching of foliar and soil nutrients [15,16,42]. Consequently, if it were not for this slow litter decomposition, there would possibly be ecosystems with leached, oligotrophic, and nutrient-poor soils, like most tropical forests [77].

The research of Valente et al. [60] concludes that litterfall production is important in degraded areas to ensure the nutrient return to the soil and suggests that the cultivation of a mixture of native trees contributes to producing higher annual litterfall, and can be a promising option for reactivation of nutrient cycling and organic matter formation in mined areas [60]. Likewise, León et al. [83] consider that a passive restoration strategy for degraded ecosystems can be via the litter mass accumulation on the ground since this allows the reactivation of the biogeochemical cycle of the ecosystem. In addition, León and Osorio [48] conclude that one of the main mechanisms of passive restoration of ecosystems degraded by open pit mining is through the recovery of nutrient recycling (litter production and decomposition), which is favored by the litter mass accumulation on the ground of the recovering ecosystem, as evidenced in ecosystems degraded by mining in the Pacific. In conclusion, after mining in the Pacific, the rate of leaf litter decomposition was reduced; however, the litterfall production and litter mass accumulation on the soil increased, thereby favoring the conditions for the slow recovery of the degraded ecosystem.

Influence of Mining on Foliar Nutrient Content

In mature forests of the Colombian Pacific, foliar nutrient content was mostly low; only N and Ca presented high foliar percentages (Table S2). Particularly, the high foliar N content possibly occurs due to the high levels of precipitation and humidity that favor the rates of atmospheric N fixation carried out by bacteria (nitrifying and ammonifying) free or in symbiosis with plants of the Fabaceae family [8,19,41,54]. This symbiosis is carried out with legumes such as *Inga* sp., *Enterolobium cyclocarpum*, *Inga coruscans*, *Hymenaea oblongifolia*, *Ormosia* *colombiana*, and *Andira inermis* [65]. Also, another factor that could explain the high percentage of foliar N is the high content of total N in the soil [77] since this nutrient has shown high content in the soil [16]. In this sense, Wood et al. [38] determined that in tropical forests, a higher nutrient content in the soil tends to generate a higher percentage of nutrient content in the leaves. In summary, the high contents of total N in the soil explain the highest percentage of its foliar content in Pacific forests.

The levels of foliar N recorded in forests of the Colombian Pacific (N = 1.39%) are within the range reported for low-altitude tropical humid forests between 0.58 and 2.52% [38,77]. Likewise, the values reported for foliar Ca in this study (Ca = 2.89%) are within the range of between 0.15 and 3.1% reported for tropical forests [38]. Surely, these high foliar Ca contents are explained by the high Ca content in the soil, as has been recorded in other studies [38], and due to the characteristics of low mobility of this mineral inside the plants [71], which has been evidenced mainly in nutrient retranslocation processes, in which the percentages of foliar Ca have been high prior to senescence [77]. In conclusion, it was noted that foliar N and Ca contents are high, and are possibly due to the influence of factors such as species composition (legumes), activity of atmospheric N-fixing bacteria, and soil fertility (availability of N and Ca). However, foliar N and Ca contents decreased significantly in post-mining forests; this reduction is surely due to nutrient relocation pro- cesses prior to leaf senescence [55], and as a conservation strategy of nutrients in disturbed environments [77].

In post-mining forests, foliar contents of P, K, Mg, Fe, Cu, Mn, and Zn increased (Figure 4), contrary to what was observed in the percentages of foliar N and Ca. These higher foliar nutrient contents are surely explained by the fact that with open pit mining, the availability of these nutrients in the soil increased [22], due to the degradation (weathering) of rocks by the action of the machines [57], and with this, the absorption of minerals by the plants surely increased [55], and, consequently, the foliar nutrient content, similar to what was recorded in

previous studies, in which a higher nutrient content has been determined in plants that grow on soils rich in these nutrients [38,71]. In particular, foliar P presented an average value of 0.11% in post-mining forests, which is within the range of between
0.01 and 0.32% reported for tropical forests [38]. However, foliar P values were so high in post-mining forests that only average foliar P values of 0.24% and 0.32% were recorded in high rainfall (>5000 mm annually) tropical forests in India [84], and reports of moderately fertile tropical forests (leaf P = 0.12%–0.15%) [77] were higher than those presented in this study. This shows that mining activity generates atypical conditions of P content (foliar and edaphic) in the ecosystem.

Although foliar P values of post-mining litter are considered high for tropical rain- forests [38,77], this nutrient affects the litter decomposition rate, probably because, stoi- chiometrically, its proportion with respect to the percentage of foliar N was very low (N/P ratio = 11.0), while in mature forests, the N/P ratio was higher (N/P ratio = 46.0), which could possibly facilitate the decomposition of leaf litter [12,41,55]. These values of the leaf N/P ratio are within the range reported for tropical rainforests of between 4.16 and
100.0 [19,38,77]. However, the results of the present study corroborate what was found in Amazonian forests, where the N/P ratio increased with succession age [19], similar to this study. This increase in the N/P ratio with age denotes that the trees translocate more foliar P before leaf fall as a nutrient conservation mechanism [19].

The content of foliar K (0.24%) was within the range of between 0.15 and 0.85% reported for tropical forests [38]. In addition, the percentage of foliar Mg (0.26%) was between 0.11 and 0.90%, reported for tropical forests [38,77]. However, in both cases (K and Mg), the values were lower than most foliar nutrient values reported in tropical rainforests [38,77]. These low values of foliar K and Mg are surely due to the influence of the high precipitation of the region (>8000 mm annually); therefore, according to the studies by Santiago et al. [42], increases in precipitation generate significant reductions in the foliar contents of P, Ca, K, and Mg in low-altitude tropical forests.

For its part, the foliar percentage of Ca (0.68%) post-mining was within the range reported for tropical forests, between 0.15 and 3.1% [38]. However, these post-mining foliar Ca values were higher than those reported for tropical humid forests with infertile oxisols/ultisols soils with ranges between 0.19 and 0.50% [77]. This high foliar availability of Ca, despite the possible translocation prior to leaf senescence [55], is possibly due to the high availability of the mineral in the soil after mining, which is similar to what was recorded by Proctor (1984) in tropical rainforests with calcareous soils where foliar Ca levels were extremely high (0.31%), due to the influence of its content in the soil [38], similar to what was reported for post-mining areas.

Influence of Mining on Nutrient Use Efficiency (NUE)

Mining increased the NUE of N, P, and K in Pacific rainforests. This NUE shows the nutrients that are being best used in the ecosystem. Said NUE shows the capacity of forest ecosystems to absorb and use nutrients to obtain greater productivity. Therefore, NUE involves three main processes in plants: nutrient uptake, assimilation, and utilization [12]. Consequently, the need for plants to use nutrients in altered environments, such as post- mining forests, is evident, since it is necessary to recover the functionality of ecosystems and maximize nutrient cycling and productivity [12]. In summary, the NUE evidenced the multiple nutrient limitations that have post-mining forests, while it denoted the Ca limitation in mature forests. In this sense, Vitousek [33] denoted that the amount of fine litterfall was also significantly correlated with phosphorus concentrations in moist and wet lowland tropical forests; these analyses suggested that phosphorus but not nitrogen availability limits litterfall in a substantial subset of intact tropical forests [33].

Consequently, sites on old oxisols and ultisols, especially those in

Amazonia, appear to be particularly low in available phosphorus [33]. For this reason, it was hypothesized that available P was the main limiting factor in the productivity of lowland tropical rain- forests [33,39]. However, this hypothesis of limitation by available P has been little tested experimentally in tropical rainforests [37]. Likewise, the limitation that soil N has on litter production in mature tropical rainforests of the Chocó biogeographic region was recently noted [66], which shows a limitation by different nutrients, not only by P in tropical rain- forests. Therefore, in this study, the NUE-Ca shows the Ca that is best used in mature forests, evidencing a possible limitation due to this nutrient. Finally, N, P, and K in post-mining rainforests in the Pacific show a limitation by multiple nutrients in post-mining areas, as has been recently evidenced in fertilization experiments [66]. In summary, through the NUE, it was possible to demonstrate changes in nutrient limitations through the succession of tropical rainforests.

Conclusions

An increase in post-mining nutrient cycling was noted (Figure S1) as a strategy for nutrient conservation, recovery of functioning, and productivity in degraded Pacific ecosys- tems. This recovery of nutrient recycling is essential to increase net primary productivity, carbon capture, and biomass, and with this, contribute significantly to the recovery of forest biodiversity and the mitigation of global climate change. Consequently, it is expected that in the future, if mining continues in the region, productivity and nutrient recycling will be altered.

In general, it is noted that in the Colombian Pacific region, and in the Latin Amer- ican basins in which open pit mining is carried out, the recycling of nutrients and theproductivity of the ecosystem will continue to be altered. This affects the dynamics of the forest and the function of these ecosystems in mitigating global climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www. mdpi.com/article/10.3390/f15071222/s1, Table S1: litter production, decomposition and mass on the ground in tropical rainforests; Table S2: litter nutrient content in tropical rainforests; Figure S1: synthesis of nutrients cycling in mature and post-mining tropical rain forests (mature and post- mining) of the Colombian Pacific.

Author Contributions: Conceptualization, H.Q.M., J.J.T.-T., and D.P.-A.; methodology, H.Q.M.; software, J.J.T.-T.; validation, H.Q.M., J.J.T.-T., and D.P.-A.; formal analysis, H.Q.M., J.J.T.-T., and D.P.-A.; investigation, H.Q.M. and J.J.T.-T.; resources, H.Q.M.; data curation, H.Q.M. and J.J.T.-T.; writing—original draft preparation, H.Q.M. and J.J.T.-T.; writing—review and editing, H.Q.M., J.J.T.-T., and D.P.-A.; visualization, H.Q.M.; supervision, H.Q.M.; project administration, H.Q.M.; fund- ing acquisition, H.Q.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was financed for the Ministry of Science, Technology, and Innovation (CODE 1128-852-72243).

Data Availability Statement: The data are not publicly available due to restrictions, such as containing information that could compromise the privacy of research participants. But they can be supplied on request.

Acknowledgments: This research was financed with the project entitled: Evaluación del efecto de la fertilización del suelo sobre la producción neta del ecosistema en áreas degradadas por la minería, como estrategia para potenciar el secuestro de carbono y la venta de servicios ambientales en el Chocó Biogeográfico (CODE 1128-852-72243), presented by the Universidad Tecnológica del Chocó "D.L.C.", Universidad Nacional de Colombia, the University of Valladolid (Spain), Instituto de Investigaciones del Pacífico, and SENA Chocó, and approved by the Ministry of Science, Technology, and Innovation. The APC was funded by the authors and the Universidad Nacional de Colombia (currently in consortium Colombia) to which the second author is linked.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Wright, S.J. The future of tropical forests. *Ann. N. Y. Acad. Sci.* **2010**, *1195*, 1–27. [CrossRef] [PubMed]
2. Groombridge, B.; Jenkins, M.D. *World Atlas of Biodiversity Earth's Living Resources in the 21st Century*; University of California: Berkeley, LA, USA, 2003.
3. FAO; UNEP. *The State of the World's Forests 2020. Forests, Biodiversity and People*; FAO: Rome, Italy; UNEP: Athens, Greece, 2020. [CrossRef]
4. Wright, S.J. Tropical forests in a changing environment. *Trends Ecol. Evol.* **2005**, *20*, 553–560. [CrossRef]
5. Field, C.B.; Behrenfeld, M.J.; Randerson, J.T.; Falkowski, P. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* **1998**, *281*, 237–240. [CrossRef]
6. Intergovernmental Panel on Climate Change—IPCC. *Climate Change 2014: Synthesis Report*; Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Chang; Core Writing Team, Pachauri, R.K., Meyer, L.A., Eds.; IPCC: Geneva, Switzerland, 2014; p. 151. Available online: https://www.ipcc.ch/report/ar5/syr/ (accessed on 15 May 2024).
7. Paoli, G.; Curran, L. Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo. *Ecosystems* **2007**, *10*, 503–518. [CrossRef]
8. Cleveland, C.C.; Townsend, A.R.; Taylor, P.; Alvarez-Clare, S.; Bustamante, M.; Chuyong, G.; Dobrowski, S.Z.; Grierson, P.; Harms, K.E.; Houlton, B.Z.; et al. Relationships among net primary productivity, nutrients and climate in tropical rain forest: A pan-tropical analysis. *Ecol. Lett.* **2011**, *14*, 939–947. [CrossRef] [PubMed]
9. Whitmore, T.C. *An Introduction to Tropical Rain Forests*, 2nd ed.; Oxford

University Press: Oxford, UK, 1998.

10. Jordan, C.F. *Nutrient Cycling in Tropical Forest Ecosystems: Principles and Their Application in Management and Conservation*, 1st ed.; Wiley & Sons: Chichester, UK, 1985; 190p.

11. Montagnini, F.; Jordán, C.F. Reciclaje de Nutrientes. In *Ecología y Conservación de Bosques Neotropicales*; Guariguata, M., Kattan, Y., Eds.; Libro Universitario Regional (LUR): San José, CA, USA, 2002; pp. 167–192.

12. Alvarado, A. Plant Nutrition in Tropical Forestry. In *Tropical Forestry Handbook*; Pancel, L., Köhl, M., Eds.; Springer: Berlin/Heidelberg, Germany, 2015. [CrossRef]

13. Metcalfe, D.B.; Asner, G.P.; Martin, R.E.; Silva, J.E.; Huasco, W.H.; Farfán, F.F.; Carranza-Jimenez, L.; Galiano, D.F.; Baca, L.D.; Sinca, F.; et al. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecol. Lett.* **2014**, *17*, 324–332. [CrossRef]

14. Foster, N.W.; Bhatti, J.S. Forest Ecosystems: Nutrient Cycling. In *Encyclopedia of Soil Sciences*; CRC Press: Boca Raton, FL, USA, 2006; pp. 718–721.

15. Austin, A.T.; Vitousek, P.M. Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai'i. *J. Ecol.* **2000**, *88*, 129–138. [CrossRef]

16. Quinto, H.; Moreno, F.H. Precipitation effects on soil characteristics in tropical rain forests of the Chocó biogeographical region. *Rev. Fac. Nac. Agron. Medellín* **2016**, *69*, 7813–7823. [CrossRef]

17. Walker, T.W.; Syers, J.K. The fate of phosphorus during pedogenesis. *Geoderma* **1976**, *15*, 1–19. [CrossRef]

18. Guariguata, M.R.; Ostertag, R. Neotropical secondary succession: Changes in structural and functional characteristics. *For. Ecol. Manag.* **2001**, *148*, 185–206. [CrossRef]

19. Davidson, E.A.; de Carvalho, C.J.; Figueira, A.M.; Ishida, F.Y.; Ometto, J.P.; Nardoto, G.B.; Sabá, R.T.; Hayashi, S.N.; Leal, E.C.; Vieira, I.C.; et al.

Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* **2007**, *447*, 995–998. [CrossRef] [PubMed]

20. Walker, L.R.; del Moral, R. Lessons from primary succession for restoration of severely damaged habitats. *Appl. Veg. Sci.* **2008**, *12*, 55–67. [CrossRef]

21. Dalling, J.W.; Heineman, K.; Lopez, O.R.; Wright, S.J.; Turner, B.L. Nutrient Availability in Tropical Rain Forests: The Paradigm of Phosphorus Limitation. In *Tropical Tree Physiology*; Tree Physiology; Goldstein, G., Santiago, L., Eds.; Springer: Cham, Switzerland, 2016; Volume 6. [CrossRef]

22. Quinto, H.; Ayala-Vivas, G.; Gutiérrez, H. Contenido de nutrientes, acidez y textura del suelo en áreas degradadas por la minería en el Chocó biogeográfico. *Rev. Acad. Colomb. Cienc. Exactas Físicas Nat.* **2022**, *46*, 514–528. [CrossRef]

23. Vitousek, P.; Porder, S.; Houlton, B.Z.; Chadwick, O.A. Terrestrial Phosphorus Limitation: Mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* **2010**, *20*, 5–15. [CrossRef] [PubMed]

24. Vitousek, P.M.; Walker, L.R.; Whiteaker, L.D.; Matson, P.A. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* **1993**, *23*, 197–215. [CrossRef]

25. Li, Y.; Yang, F.; Ou, Y.; Zhang, D.; Liu, J.; Chu, G.; Zhang, Y.; Otieno, D.; Zhou, G. Changes in forest soil properties in different successional stages in lower tropical China. *PLoS ONE* **2013**, *8*, e81359. [CrossRef] [PubMed]

26. Hedin, L.O.; Brookshire, J.; Menge, D.; Barron, A.R. The Nitrogen Paradox in Tropical Forest Ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 613–635. [CrossRef]

27. Chazdon, R.L. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* **2003**, *6*, 51–71. [CrossRef]

28. Figueroa, M.L.; Martínez, M.R.; Ortiz, C.A.; Fernández, D. Influencia de los factores formadores en las propiedades de los suelos en la Mixteca, Oaxaca, México. *Terra Latinoam.* **2018**, *36*, 287–299. [CrossRef]

29. Schuur, E.A. Productivity and global climate revisited: The sensitivity of

tropical forest growth to precipitation. *Ecology* **2003**, *84*, 1165–1170. [CrossRef]
30. Quinto, H.; Ramos, Y.A.; Abadía, D. Cuantificación de la caída de hojarasca como medida de la productividad primaria neta en un Bosque Pluvial Tropical en Salero, Unión Panamericana, Chocó—Colombia. *Rev. Investig. Biodivers. Desarro.* **2007**, *26*, 28–41.
31. Clark, D.A.; Brown, S.; Kicklighter, D.W.; Chambers, J.D.; Thomlinson, J.R.; Ni, J. Measuring net primary production in forest: Concepts and field methods. *Ecol. Appl.* **2001**, *11*, 356–370. [CrossRef]
32. Chave, J.; Navarrete, D.; Almeida, S.; Álvarez, E.; Aragão, L.E.; Bonal, D.; Châtelet, P.; Silva-Espejo, J.E.; Goret, J.Y.; von Hildebrand, P.; et al. Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* **2010**, *7*, 43–55. [CrossRef]
33. Vitousek, P.M. Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* **1984**, *65*, 285–298. [CrossRef]
34. Quinto, H.; Mena-Domínguez, Y.; Valoyes-Hinestroza, H. Relación entre la producción de hojarasca y las condiciones edáficas en bosques pluviales tropicales del Chocó Biogeográfico, Colombia. *Actual. Biológicas* **2017**, *39*, 29–40. [CrossRef]
35. LeBauer, D.S.; Treseder, K.K. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **2008**, *89*, 371–379. [CrossRef] [PubMed]
36. Wright, J.; Yavitt, J.; Wurzburger, N.; Turner, B.; Tanner, E.; Sayer, E.; Santiago, L.; Kaspari, M.; Hedin, L.; Harms, K.; et al. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* **2011**, *92*, 1616–1625. [CrossRef] [PubMed]
37. Cunha, H.F.; Andersen, K.M.; Lugli, L.F.; Santana, F.D.; Aleixo, I.F.; Moraes, A.M.; Garcia, S.; Di Ponzio, R.; Mendoza, E.O.; Brum, B.; et al. Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature* **2022**, *608*, 558–562. [CrossRef] [PubMed]
38. Wood, T.E.; Lawrence, D.; Clark, D.A. Determinants of leaf litter nutrient

cycling in a tropical rain forest: Soil fertility versus topography. *Ecosystems* **2006**, *9*, 700–710. [CrossRef]

39. Wright, S.J.; Turner, B.L.; Yavitt, J.B.; Harms, K.E.; Kaspari, M.; Tanner, E.V.J.; Bujan, J.; Griffin, E.A.; Mayor, J.R.; Pasquini, S.C.; et al. Plant responses to fertilization experiments in lowland, species-rich, tropical forests. *Ecology* **2018**, *99*, 1129–1138. [CrossRef]

40. Swift, M.J.; Heal, O.W.; Anderson, J.M. *Decomposition in Terrestrial Ecosystems*; University of California Press: Oxford, UK, 1979.

41. Chapin, F.S., III; Matson, P.A.; Mooney, H.A. *Principles of Terrestrial Ecosystem Ecology*; Springer: New York, NY, USA, 2002.

42. Santiago, L.S.; Schuur, E.A.G.; Silvera, K. Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama. *J. Trop. Ecol.* **2005**, *21*, 461–470. [CrossRef]

43. Powers, J.S.; Montgomery, R.A.; Adair, E.C.; Brearley, F.Q.; Dewalt, S.J.; Castanho, C.T.; Chave, J.; Deinert, E.; Ganzhorn, J.U.; Gilbert, M.E.; et al. Decomposition in tropical forests: A pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *J. Ecol.* **2009**, *97*, 801–811. [CrossRef]

44. Blanco, J.A.; Durán, M.; Luquin, J.; San Emeterio, L.; Yeste, A.; Canals, R.M. Soil C/N ratios cause opposing effects in forests compared to grasslands on decomposition rates and stabilization factors in southern European ecosystems. *Sci. Total Environ.* **2023**, *888*, 164118. [CrossRef] [PubMed]

45. Schuur, E.A. The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. *Ecosystems* **2001**, *4*, 259–273. [CrossRef]

46. Del Valle, J.I. Descomposición de la hojarasca fina en bosques pantanosos del Pacífico colombiano. *Interciencia* **2003**, *28*, 148–153.

47. Wieder, W.R.; Cleveland, C.C.; Townsend, A.R. Controls over leaf litter decomposition in wet tropical forests. *Ecology* **2009**, *90*, 3333–3341. Available online: https://www.jstor.org/stable/25660981 (accessed on 28 May 2024).

[CrossRef] [PubMed]
48. León, J.D.; Osorio, N.W. Role of litter turnover in soil quality in tropical degraded lands of Colombia. *Sci. World J.* **2014**, *2014*, 693981. [CrossRef] [PubMed]
49. Gaspar-Santos, E.S.; González-Espinosa, M.; Ramírez-Marcial, N.; Álvarez-Solís, J.D. Acumulación y descomposición de hojarasca en bosques secundarios del sur de la Sierra Madre de Chiapas, México. *Bosque* **2015**, *36*, 467–480. [CrossRef]
50. Paudel, E.; Dossa, G.G.; de Blecourt, M.; Beckschafer, P.; Xu, J.; Harrison, R.D. Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. *Ecosphere* **2015**, *6*, 267. [CrossRef]
51. Wongprom, J.; Poolsiri, R.; Diloksumpun, S.; Ngernsaengsaruay, C.; Tansakul, S.; Chandaeng, W. Litterfall, litter decomposition and nutrient return of rehabilitated mining areas and natural forest in Phangnga Forestry Research Station, Southern Thailand. *Biotropia* **2022**, *29*, 69–80. [CrossRef]
52. Fang, H.; Mo, J.; Peng, S.; Li, Z.; Wang, H. Cumulative effects of nitrogen additions on litter decomposition in three tropical forests in southern China. *Plant Soil* **2007**, *297*, 233–242. [CrossRef]
53. Xiaogai, G.; Lixiong, Z.; Wenfa, X.; Zhilin, H.; Xiansheng, G.; Benwang, T. Effect of litter substrate quality and soil nutrients on forest litter decomposition: A review. *Acta Ecol. Sin.* **2013**, *33*, 102–108. [CrossRef]
54. Sathya, A.; Vijayabharathi, R.; Gopalakrishnan, S. Soil microbes: The invisible managers of soil fertility. In *Microbial Inoculants in Sustainable Agricultural Productivity*; Singh, D.P., Singh, H.B., Prabha, R., Eds.; Springer: Telangana, India, 2016.
55. Lambers, H.; Chapin, F.S., III; Pons, T.L. *Plant Physiological Ecology*, 2nd ed.; Springer Science Business Media, LLC: New York, NY, USA, 2008. [CrossRef]
56. Primack, R.B.; Vidal, O. *Introducción a la Biología de la Conservación*; Ediciones Científicas Universitarias: México, Mexico, 2019.

57. Ángel, J.; Ordoñez, M.; Olivero, J.; Echavarría, C.; Ayala, H.; Cabrera, M. *Consideraciones Sobre la Minería en el Departamento del Chocó y Recomendaciones para Mejorar la Gestión*; Geopatrimonio—Universidad de Cartagena—IIAP—WWF: Cali, Colombia, 2019; 58p.

58. Valois, H.C. Sucesión Primaria y Ecología de la Revegetación de Selvas Degradadas por Minería en el Chocó, Colombia: Bases Para su Restauración Ecológica. Ph.D. Thesis, Universidad de Valladolid, Valladolid, Spain, 2016.

59. Ramirez, G.; Ledezma, E. Efectos de las actividades socio-económicas (minería y explotación maderera) sobre los bosques del departamento del Chocó. *Rev. Investig. Biodivers. Desarro.* **2007**, *26*, 58–65.

60. Valente, F.D.A.; Castro, M.F.; Lustosa, J.F.; Lopes, A.T.; Borges, S.R.; Gomes, L.C.; Neves, J.C.L.; Silva, I.R.; Oliveira, T.S. Litterfall production, decomposition and litter nutrient contents in a mined area revegetated with different forest species. *Rev. Bras. Cienc. Solo.* **2023**, *47*, e0220122. [CrossRef]

61. Digna, T. *La Minería en Chocó en Clave de Derechos. Investigación y Propuestas para Convertir la Crisis Socio-Ambiental en paz y Justicia Territorial*; Centro de Estudios para la Justicia Social (CEJS): Bogotá, Colombia, 2016. Available online: https:// justiciaambientalcolombia.org/reporte-la-mineria-en-choco/ (accessed on 1 June 2024).

62. Poveda, I.C.; Rojas, C.; Rudas, A.; Rangel, O. El Chocó Biogeográfico: Ambiente Físico. In *Colombia Diversidad Biótica IV*; El Chocó Biogeográfico/Costa Pacífica; Rangel, O., Ed.; Universidad Nacional de Colombia: Bogotá, Colombia, 2004; 1024p.

63. Quinto, H.; Moreno, F. Dinámica de la biomasa aérea en un bosque pluvial tropical del Chocó Biogeográfico. *Rev. Fac. Nac. Agron. Medellín* **2011**, *64*, 5917–5936.

64. Quinto, H.; Hurtado, D.; Arboleda, J. Influencia de las condiciones edáficas sobre la dominancia y diversidad de árboles en bosques pluviales tropicales del Chocó biogeográfico. *Rev. Biol. Trop.* **2019**, *67*, 1278–1291. [CrossRef]

65. Ramírez, G.; Rangel-Ch, J. Sucesión vegetal en áreas de minería a cielo

abierto en el bosque pluvial tropical del departamento del Chocó, Colombia. *Rev. Acad. Colomb. Cienc. Exactas Físicas Nat.* **2019**, *43*, 673–688. [CrossRef]

66. Quinto, H.; Cuesta, H.V.; Abadía, D.P. Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian Pacific. *Rev. Bras. Cienc. Solo* **2024**, *48*, e0230053. [CrossRef]

67. Quinto, H.; Rivas-Urrutia, Y.; Palacios-Murillo, N. Fine root biomass and its relationship with the soil in degraded areas by mining in biogeographic Chocó. *Rev. Fac. Nac. Agr. Med.* **2023**, *76*, 2–15. [CrossRef]

68. Quinto, H.; Ramos, Y.A. Descomposición de hojarasca en un bosque pluvial tropical intervenido en el municipio de Lloró, Chocó, Colombia. *Rev. Investig. Biodivers. Desarro.* **2009**, *28*, 32–43.

69. Yeong, K.L.; Reynolds, G.; Hill, J.K. Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo. *Biotropica* **2016**, *48*, 443–452. [CrossRef]

70. Olson, J.S. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **1963**, *44*, 322–331. [CrossRef]

71. Osorio, N.W. *Manejo de Nutrientes en Suelos del Trópico*, 2nd ed.; Editorial L. Vieco S.A.S.: Medellín, Colombia, 2014; 416p.

72. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2013. Available online: http://www.r-project.org (accessed on 29 May 2024).

73. Ruíz, A.R.; Schlebusch, J.; Howald, C.; Flórez, J.A. Impactos de la Minería en el Pacífico Colombiano. Observatorio Pacífico y Territorio–OPT. Coordinación Regional del Pacífico Colombiano–CRPC. Editorial Nuevo Milenio, 2018; 257p. Available online: http://pacificocolombia.org (accessed on 29 May 2024).

74. Torres-Torres, J.J.; Quinto, H.; Medina, H.H. Diversidad de especies leñosas y su relación con variables ambientales en bosques post-minería del Chocó Biogeográfico. *Bol. Cient. Mus. Hist. Nat. Univ. Caldas* **2023**, *27*, 13–29. [CrossRef]

75. Shetty, R.; Vidya, C.S.N.; Prakash, N.B.; Lux, A.; Vaculik, M. Aluminum toxicity in plants and its possible mitigation in acid soils by biochar: A review. *Sci. Total Environ.* **2021**, *765*, 142744. [CrossRef] [PubMed]

76. Chandra, J.; Keshavkant, S. Mechanisms underlying the phytotoxicity and genotoxicity of aluminum and their alleviation strategies: A review. *Chemosphere* **2021**, *278*, 130384. [CrossRef] [PubMed]

77. Vitousek, P.M.; Sanford, R.L. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* **1986**, *17*, 137–167. [CrossRef]

78. Moreno, F.; Oberbauer, S.F. Dynamics of Soil Carbon in Primary and Secondary Tropical Forests in Colombia. In *Managing Forest Ecosystems: The Challenge of Climate Change. Managing Forest Ecosystems*; Bravo, F., Jandl, V., LeMay, V., von Gadow, K., Eds.; Springer: Berlin/Heidelberg, Germany, 2008; Volume 17, pp. 283–296. [CrossRef]

79. Mosquera, R.S.; Valois, H.; Vasco-Palacios, A.M. Rol de los hongos micorrízicos arbusculares durante la sucesión natural de áreas impactadas por minería en un bosque pluvial tropical del Chocó, Colombia. *Bosque* **2023**, *44*, 617–627. [CrossRef]

80. Chapin, F.S., III. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* **1980**, *11*, 233–260. [CrossRef]

81. Grau, J.; Ferry, B.V.; Freycon, L.; Blanc, M.; Desprez, C.; Baraloto, J.; Chave, L.; Descroix, A.; Dourdain, S.; Guitet, I.A.; et al. Nutrient-cycling mechanisms other than the direct absorption from soil may control forest structure and dynamics in poor Amazonian soils. *Sci. Rep.* **2017**, *7*, 45017. [CrossRef]

82. Hobbie, S.E. Plant species effects on nutrient cycling: Revisiting litter feedbacks. *Trends Ecol. Evol.* **2015**, *30*, 357–363. [CrossRef]

83. León, J.D.; Caicedo-Ruiz, W.; Castellanos-Barliza, J. Reactivation of nutrient cycling in an urban tropical dry forest after abandonment of agricultural activities. *Rev. Chapingo Ser. Cienc. For. Ambiente* **2021**, *27*, 355–365. [CrossRef]

84. Rai, S.N.; Proctor, J. Ecological studies on four rainforests in Karnataka, India: II. *Litterfall. J. Ecol.* **1986**, *74*, 455–463. [CrossRef]

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Conclusiones

La minería a cielo abierto altera significativamente los ciclos de nutrientes, la producción de hojarasca y la biomasa aérea de los bosques tropicales del Pacífico colombiano.

Aunque los bosques post-mineros muestran una lenta recuperación de biomasa y productividad, presentan un aumento en la producción de hojarasca, lo que favorece la acumulación de materia orgánica y nutrientes en el suelo, contribuyendo a la regeneración del ecosistema.

La recuperación de la biomasa aérea y la PPN en los bosques post-mineros depende de múltiples factores, incluyendo la fertilidad del suelo, la riqueza de especies y la edad sucesional. Los contenidos de N, P, Ca y Mg en el suelo son determinantes clave para la restauración del ciclo de nutrientes y la productividad en los bosques post-minería.

Efectos en el contenido de nutrientes del suelo

La minería aumentó significativamente el contenido de nutrientes como fósforo (P), potasio (K), calcio (Ca) y magnesio (Mg) en los suelos post-minería. Esto se debe a la liberación de nutrientes durante la meteorización de las rocas provocada por la actividad minera. Sin embargo, la minería también incrementó los niveles de aluminio (Al) en el suelo, lo cual podría generar toxicidad y afectar negativamente el crecimiento de las plantas (Davidson et al., 2004; Guariguata y Ostertag, 2001).

Influencia en la producción y descomposición de hojarasca

La producción de hojarasca fue mayor en los bosques post-minería debido a la mayor disponibilidad de nutrientes en el suelo. No obstante, la tasa de descomposición de la hojarasca fue menor en comparación con los bosques maduros, lo que indica un mecanismo de conservación de nutrientes en ecosistemas perturbados (Vitousek y Sanford, 1986). Esto generó una mayor acumulación de masa de hojarasca en el suelo post-minería, favoreciendo la acumulación de MO y nutrientes (Montagnini y Jordan, 2005).

Contenido de nutrientes foliares

En los bosques maduros, los contenidos foliares de nitrógeno (N) y calcio (Ca) fueron superiores, mientras que en los bosques post-minería se encontraron mayores contenidos de potasio (K), magnesio (Mg), fósforo (P) y otros micronutrientes (Osorio, 2021). Esta diferencia se debe a los procesos de reubicación de nutrientes previos a la abscisión de las hojas en árboles post-minería, como estrategia de conservación de nutrientes en ambientes perturbados (Vitousek y Sanford, 1986).

Eficiencia en el uso de nutrientes (EUN)

La EUN de nitrógeno (N), fósforo (P) y potasio (K) fue mayor en los bosques post-minería, mientras que la EUN de calcio (Ca) fue superior en los bosques maduros (Vitousek, 1984). Esto refleja las diferencias en la disponibilidad de nutrientes y las estrategias de conservación entre ambos tipos de bosques.

Finalmente, el estudio demuestra que la minería a cielo abierto tiene un impacto significativo en los bosques húmedos tropicales, afectando tanto la estructura del suelo como los procesos ecológicos esenciales para el funcionamiento del ecosistema. Aunque la minería aumenta la disponibilidad de ciertos nutrientes, también genera condiciones que pueden limitar la recuperación del ecosistema, como la toxicidad por aluminio. La mayor producción de hojarasca y la menor tasa de descomposición en los bosques post-minería indican una acumulación de materia orgánica que puede favorecer la recuperación a largo plazo, pero que también refleja un estado de conservación de nutrientes.

Para mitigar estos efectos y promover la restauración de los bosques post-minería, es esencial desarrollar estrategias de manejo sostenible que incluyan la rehabilitación del suelo y la reforestación con especies nativas adaptadas a las condiciones edáficas y climáticas de la región. Estos esfuerzos contribuirán no solo a la recuperación de la biodiversidad y la funcionalidad del ecosistema, sino también a la mitigación del cambio climático global mediante el secuestro de carbono.

Universidad de Valladolid

Escuela de Doctorado Universidad de Valladolid

Bibliografía

Ángel, J. M. Ordoñez, J. Olivero, C. Echavarría, H. Ayala, M. Cabrera. (2019). Consideraciones sobre la minería en el departamento del Chocó y recomendaciones para mejorar la gestión. Geopatrimonio – Universidad de Cartagena - IIAP - WWF. Páginas 58. Cali - Colombia.

Beer, C. , Reichstein, M. , Tomelleri, E. , Ciais, P. , Jung, M. , Carvalhais, N. , Rödenbeck, C. , Arain, M. A. , Baldocchi, D. , Bonan, G. B. , Bondeau, A. , Cescatti, A. , Lasslop, G. , Lindroth, A. , Lomas, M. , Luyssaert, S. , Margolis, H. , Oleson, K. W. , Roupsard, O. , … Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. Science, 329(5993), 834–838. 10.1126/science.1184984

Bonan, G. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science 320: 1444-1449(2008). DOI:10.1126/science.1155121

Cleveland CC, AR Townsend, P Taylor, S Alvarez-Clare, M Bustamante, G Chuyong, SZ Dobrowski, P Grierson, KE Harms, BZ Houlton, A Marklein, W Parton, S Porder, SC Reed, CA Sierra, WL Silver, EVJ Tanner, WR Wieder. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecology Letter 14(9): 939-947. https://doi.org/10.1111/j.1461-0248.2011.01658.x

Faber-Langendoen D, A Gentry. 1991. The structure and diversity of rain forests at Bajo Calima, Chocó Region, Western Colombia. Biotropica 23(1): 2-11. https://doi.org/10.2307/2388682

Clark, D. A., S. Brown, D. W. Kicklighter, J. D. Chambers, J. R. Thomlinson & J. Ni. 2001a. Measuring Net Primary Production in Forest: Concepts and Field Methods. Ecological Aplications 11 (2) 356 – 370.

Clark, D. A., S. Brown, D. W. Kicklighter, J. D. Chambers, J. R. Thomlinson , E. Holland & J. Ni. 2001b. Net Primary Production in Forest: An Evaluation and Sinthesis of Existing Field Data. Ecological Aplications 11 (2) 356 – 370.

Environmental Law Alliance Worldwide (ELAW). 2010. Guidebook for Evaluating Mining Project EIAs. Eugene, OR 97403. U.S.A. Pp. 110. ISBN 978-0-9821214-36. www.elaw.org

Giljum, S., Maus, V., Kuschnig, N., Luckeneder, S., Tost, M., Sonter, LJ y Bebbington, AJ (2022). Una evaluación pantropical de la deforestación causada por la minería industrial. Actas de la Academia Nacional de Ciencias (PNAS) ,https://doi

Haddad, NM, Brudvig, LA, Clobert, J., Davies, KF, Gonzalez, A., Holt, RD, ... & Townshend, JR (2015). Fragmentación del hábitat y su impacto duradero en los ecosistemas de la Tierra. Science Advances, 1(2), e1500052.

Laurance, WF (2015). La lucha de la vida silvestre en un mundo cada vez más ruidoso. Nature, 525, 7.

Lu Q, H. Liu, L. Wei, Y. Zhong, and Zhou. Z. (2024). Global prediction of gross primary productivity under future climate change. *Science of the Total Environment* 912:169239. https://doi.org/10.1016/j.scitotenv.2023.169239.

Malhi, Y., C. Doughty and Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. Phil. Trans. R. Soc. B (2011) 366, 3225–3245. doi:10.1098/rstb.2011.0062.

Montagnini, F., & Jordan, CF (2005). Ecología de los bosques tropicales: bases para la conservación y el manejo . Springer. 281 páginas.

Mori, T. (2022). Mayores impactos de la fertilización con fósforo en la actividad de la fosfatasa del suelo en los bosques tropicales que en los ecosistemas terrestres naturales no tropicales: un metaanálisis. Pedobiologia - Journal of Soil Ecology, 91-92, 150808.

Pan Y, RA Birdsey, OL Phillips, RB Jackson. 2013. The Structure, Distribution, and Biomass of the World’s Forests. Annual Review of Ecology, Evolution, and Systematics 44(1):593-622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Myers N, RA Mittermeier, CG Mittermeier, GAB da Fonseca, J Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858. https://doi.org/10.1038/35002501

Nye, P.H. 1961. Organic matter and nutrient cycles under moist tropical forest. Plant & Soil, 13: 333-346.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecol., 44:322-331.

Phillips, O. L., Y. Malhi, N. Higuchi, W. Laurance, P. Núñez, M. Vásquez, S. Laurance, L. Ferreira, M. Stern, S. Brown & J. Grace. 1998. Changes in the Carbon balance of tropical forest: Evidence from long-term plots. Science 282: 439-442.

Pratiwi, BH, Narendra, BH, Siregar, CA, Turjaman, M., Hidayat, A., Rachmat, HH, et al. (2021). Gestión y reforestación del paisaje degradado posterior a la minería en Indonesia: una revisión. Terreno , 10(658). https://doi.org/10.3390/land10060658

Primack, R., y Vidal, O. (2019). Introducción a la Biología de la Conservación. Ediciones científicas universitarias. Fondo de Cultura económica. Ciudad de México. México. 613 pp.

Quinto, H. & Moreno, F.H. 2011. Dinámica de la Biomasa Aérea en un Bosque Pluvial Tropical del Chocó Biogeográfico. Revista Facultad Nacional de Agronomía Medellín 64 (1): 5917-5936.

Quinto, H. & Moreno, F.H. 2016. Precipitation effects on soil characteristics in tropical rain forests of the Chocó biogeographical region. Revista Facultad Nacional de Agronomía Medellín 69(1): 7813-7823. Doi:10.15446/rfna.v69n1.54749.

Quinto, H., & Y.A. Ramos. 2009. Descomposición de hojarasca en un bosque pluvial tropical intervenido en el municipio de Lloró, Chocó, Colombia. Revista Institucional Universidad Tecnológica del Chocó 28: 32-43.

Quinto, H., Ramos, Y.A., & D. Abadía. 2007. Cuantificación de la caída de hojarasca como medida de la productividad primaria neta en un Bosque Pluvial Tropical en Salero, Unión Panamericana, Chocó – Colombia. Revista Institucional Universidad Tecnológica del Chocó 26: 28-41.

Quinto-Mosquera H, Moreno F. 2017. Net Primary Productivity and Edaphic Fertility in Two Pluvial Tropical Forests in the Chocó Biogeographical Region of Colombia. PLoS ONE 12 (1): e0168211. doi:10.1371/journal.pone.0168211 .

Quinto-Mosquera, H., Cuesta-Nagles, J., Mosquera-Sánchez, I., Palacios-Hinestroza, L., & Peñaloza-Murillo, H. 2013. Biomasa vegetal en zonas degradadas por minería en un bosque pluvial tropical del Chocó Biogeográfico. Revista Biodiversidad Neotropical 3(1): 53-64. http://dx.doi.org/10.18636/bioneotropical.v3i1.127.

Quinto-Mosquera, H., Mena-Domínguez, Y., & H. Valoyes-Hinestroza. 2017. Relación entre la producción de hojarasca y las condiciones edáficas en bosques pluviales tropicales del Chocó Biogeográfico, Colombia. Actualidades Biológicas, 39 (106): 29-40.

Quinto-Mosquera H, Ayala Vivas G, Gutiérrez H. (2022). Contenido de nutrientes, acidez y textura del suelo en áreas degradadas por la minería en el Chocó biogeográfico. Rev. Acad. Colomb. Cienc. Ex. Fis. Nat. 46(179):514-528. https://doi.org/10.18257/raccefyn.1615

Quinto-Mosquera H, Moreno F (2017). Net Primary Productivity and Edaphic Fertility in Two Pluvial Tropical Forests in the Chocó Biogeographical Region of Colombia. PLoS ONE 12 (1): e0168211. doi:10.1371/journal.pone.0168211.

Ramírez, G., & E. Ledezma. 2007. Efectos de las Actividades Socio-económicas (Minería y Explotación Maderera) Sobre los Bosques del Departamento del Chocó. Revista Institucional Universidad Tecnológica del Chocó 26: 58-65.

Ramirez, G., & Rangel-Ch., J. O. (2019). Sucesión vegetal en áreas de minería a cielo abierto en el bosque pluvial tropical del departamento del Chocó, Colombia. Revista De La Academia Colombiana De Ciencias Exactas, Físicas Y Naturales, 43(169), 673–688. https://doi.org/10.18257/raccefyn.896

Schuur, E.A. 2003. Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. Ecology 84:1165-1170.

Sonter, LJ, Herrera, D., Barrett, DJ, Galford, GL, Moran, CJ y Soares-Filho, BS (2017). La minería impulsa una deforestación extensiva en la Amazonia brasileña. Nature Communications, 8, 1013.

Valois-Cuesta, H. 2016. Sucesión primaria y ecología de la revegetación de selvas degradadas por minería en el Chocó, Colombia: bases para su restauración ecológica. Tesis doctoral, Universidad de Valladolid. España.

Vicente, AG (2019). ¿Se puede "secuestrar" carbono a la vez que se conserva la biodiversidad de los bosques? Revisión de la evidencia científica y recomendaciones. Revista de Investigación UNED, 11(1), S44-S47.

Walker, TW y Syers, JK (1976). El destino del fósforo durante la pedogénesis. Geoderma, 15, 1–19. Esta referencia proporciona un contexto histórico y una comprensión fundamental de la dinámica del fósforo en suelos de bosques tropicales altamente meteorizados, esencial para los debates sobre el ciclo de nutrientes.

Whitmore T.C. 1998. An Introduction to Tropical Rain Forests. Second Edition. Oxford University Press, Oxford.