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REVIEW ARTICLE

Assessing restoration strategies for the recovery of Colombian Moist Forests: a meta-analysis

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To mitigate the loss of Colombia's Moist Forests—35% of their original extent by 2021—understanding successional dynamics is critical for effective restoration. This study synthesizes data from 34 peer-reviewed articles to evaluate the efficacy of restoration methods (natural regeneration, native or exotic plantations, nucleation, remediation, agroforestry, or silvopastoral systems) in recovering vegetation structure, leaf litter, soil nutrients, and species richness. Using meta-analyses and multivariate models, we compared active restoration methods with natural regeneration, evaluated their similarity to old-growth native forests, and identified key drivers of recovery. Results showed that native plantations and silvopastoral systems accelerate vegetation structure recovery in early successions (<30 years), reaching metrics comparable to old-growth native forests, whereas natural regeneration progresses slower. Exotic plantations underperformed in vegetation recovery, reinforcing the importance of using native species for restoration. Despite differences in structural recovery, species richness (plants, birds, and insects). Soil nutrients and leaf litter accumulation showed no significant variation across restoration methods, highlighting the cost-effectiveness of natural regeneration in resilient landscapes. Environmental factors—particularly precipitation, elevation, and climatic seasonality—strongly influenced tree density, basal area, and bird richness. Succession time and prior land use activity further shaped recovery outcomes, with forest degradation exhibiting faster structural recovery. The large residual heterogeneity in the meta-analyses reflects the variability in restoration contexts, emphasizing the need for site-specific strategies: active restoration in highly degraded or fragmented landscapes and natural regeneration in well-connected, resilient regions. These insights align with national and global restoration initiatives, integrating research with diverse outcomes in tropical forest restoration.

Key words: **environmental variables, natural regeneration, plantations, species richness, succession time, vegetation structure**

Implications for Practice

- Prioritize Native Species Plantations: use native species in active restoration to accelerate vegetation recovery, as they are better adapted to local conditions and support ecological processes more effectively than exotic species.
- Leverage Natural Regeneration: in resilient areas with favorable conditions, rely on natural regeneration as a cost-effective and ecologically sound strategy, especially where connectivity to old-growth native forests exists.
- Tailor Strategies to Local Contexts: customize restoration approaches based on environmental factors (e.g. precipitation and elevation) and land use history to maximize effectiveness, using active restoration in degraded areas and natural regeneration in resilient ones. Implement continuous monitoring and adaptive management to track progress, address variability in outcomes, and refine strategies over time, ensuring long-term restoration success.

Introduction

Moist forests, as defined by Olson et al. (2001), constitute Colombia's largest biome, historically covering 75% of its continental land area prior to significant anthropogenic alteration. Recognized as a global hotspot for species diversity and endemism (Sarkar et al. 2009), this biome has faced substantial transformation, with 35% of their original extent lost by 2021 (Colombian Institute of Hydrology, Meteorology and Environmental Studies-IDEAM 2023). Key drivers of Colombian Moist Forest transformation include large-scale agriculture, cattle farming, illicit crops, and population growth (Sanchez-Cuervo & Aide 2012; González-González et al. 2021). The loss of Colombian Moist Forest underscores the urgency of restoring it through strategies aligned with national objectives, such as

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Colombia's National Development Plan (2022–2026), which targets the restoration of 1.7 million hectares of degraded ecosystems (DNP 2023), and global commitments such as the Sustainable Development Goals (UN 2015), Bonn Challenge (IUCN 2014), and the UN Decade on Ecosystem Restoration (2021–2030) (UN 2014).

Existing research extensively documents tropical forest succession (Guariguata & Ostertag 2001; Poorter et al. 2021), pointing out that succession pathways are shaped by multiple factors, including land use history, environmental variables, landscape context, human actions, and expectations (Poorter et al. 2021). However, uncertainties persist regarding recovery time and trajectory in heavily degraded areas (Florentine & Westbrooke 2004). Recent studies alert on the declining resilience in tropical forests (Flores et al. 2020; Boulton et al. 2022), suggesting that trespassing critical tipping points of degradation may require human intervention to achieve a recovery of forests (Stork et al. 2009). Additionally, addressing complex challenges like arrested successions, where natural regeneration by itself is not sufficient to recover the ecosystem to a similar state prior to disturbance, requires an understanding of the variables responsible for arresting the succession to focus restoration actions on improving these aspects (Arroyo-Rodríguez et al. 2017).

A variety of restoration strategies—such as natural regeneration, native or exotic plantations, nucleation, remediation, agroforestry, or silvopastoral systems (described in Table S1)—have been extensively studied in tropical forests, providing valuable guidance for promoting desired ecological outcomes. Plantations with native species can support natural recolonization; however, some slow-growing species—especially those dispersed by gravity or mammals—may still face challenges in establishing successfully (Suganuma & Durigan 2022). These plantations are particularly useful in highly degraded areas and also aim to improve connectivity within remnant native forests (César et al. 2018). In fragmented landscapes with existing seed dispersers and landowner support, nucleation has emerged as a cost-effective approach, achieving biodiversity and structural outcomes comparable to tree plantations with lower investment (Holl et al. 2020). Conversely, monocultures of exotic species like *Eucalyptus* can harm biodiversity, soil properties, and ecosystem functions (Iglesias-Carrasco et al. 2025). However, mixed plantations combining native and fast-growing exotic species may balance ecological recovery with economic returns, as demonstrated by Brancalion et al. (2020) in their work in the Brazilian Atlantic Forest. Natural regeneration remains the most cost-effective and ecologically beneficial strategy overall, often outperforming active restoration efforts (Crouzeilles et al. 2017). Ultimately, successful restoration depends on context, and planning should consider factors such as ecosystem resilience, land use history, connectivity, project goals, and resource availability, among others (Holl & Aide 2011).

Colombian restoration initiatives face systemic challenges, including unrealistic short-term objectives constrained by administrative timelines (Murcia et al. 2016, 2017). Most projects monitor outcomes for ≤5 years, mainly focusing on vegetation diversity inventories without a deep analysis of other components such as fauna, nutrient cycling, and hydrological functions (Garibello et al. 2021; Peña-Gonzales 2022). This lack of mid- and long-term monitoring of restoration projects prevents the assessment of the success of this practice (Murcia et al. 2016) and results often remain confined to technical reports rather than peer-reviewed literature, hindering knowledge transfer (Peña-Gonzales 2022). Furthermore, research is mainly concentrated in the Andean region, limiting insights into restoration under diverse environmental conditions (Murcia & Guariguata 2014; Garibello et al. 2021). To bridge these gaps, studies on successional forests—particularly chrono-sequences following land abandonment or conservation efforts—are critical. Such analyses enable generalizations about forest recovery by evaluating vegetation structure (e.g. basal area, canopy cover, and tree density) and species richness across taxa (plants, birds, and insects). By comparing chrono-sequences with old-growth native forests and actively restored sites under similar conditions, researchers can assess restoration efficacy and ecosystem resilience, thereby informing future project design.

This study synthesized data from peer-reviewed articles on Colombian Moist Forest successions and adjacent old-growth native forests to evaluate the recovery of vegetation structure and species richness across different restoration methods and environmental contexts. Using meta-analyses and multivariate models, we addressed three questions:

(1) Does any active restoration method (native or exotic plantations, nucleation, remediation, agroforestry, or silvopastoral systems) differ from naturally regenerated forests—under comparable environmental conditions, succession time, and land use histories—in vegetation structure (basal area, canopy cover, height, and tree density) and species richness (plants, birds, and insects)?
(2) Does any restoration method (natural regeneration, native or exotic plantations, nucleation, remediation, agroforestry, or silvopastoral systems) produce successional forests that more closely resemble old-growth native forests in terms of vegetation structure (aerial biomass, basal area, canopy cover, height, and tree density), leaf litter depth and production, soil nutrients (carbon, phosphorus, and nitrogen content), and species richness (plants, frogs, and insects)?
(3) Do environmental variables (temperature, precipitation, and elevation), succession time, prior land use activity (cattle farming, forest degradation, gold mining, and conifer plantation), or restoration methods (natural regeneration, native, or exotic plantations, remediation) explain variation in vegetation structure (tree density and basal area) and species richness (plants, birds, and insects) in successional forests?

By addressing these questions, this study aims to provide evidence-based insights into the drivers of forest recovery in

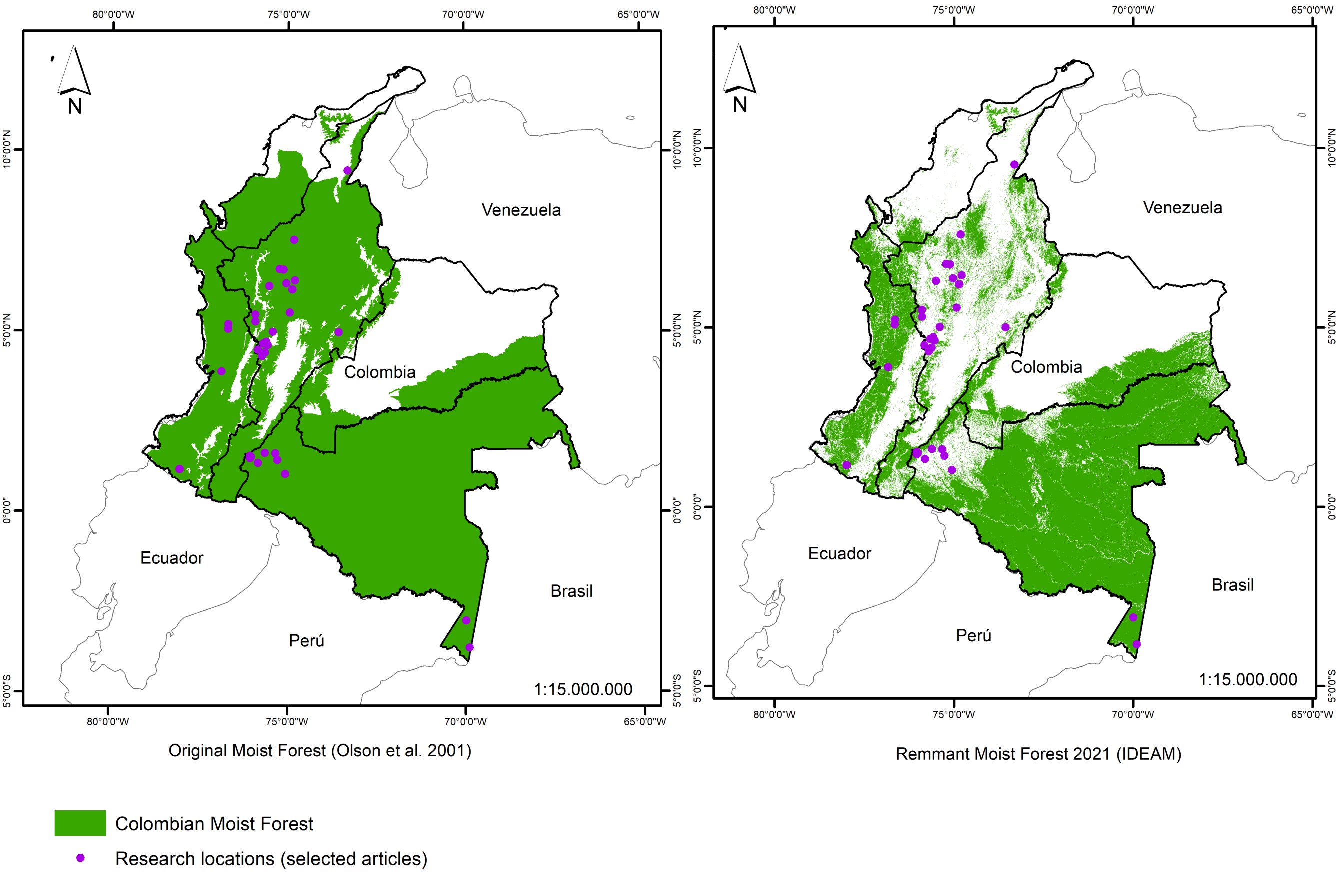
Colombian Moist Forests. Our findings are useful to inform the selection of context-specific restoration strategies that balance structural recovery, species richness gain, and costs, ultimately contributing to national and global restoration goals. We hypothesized that actively restored forests (native/exotic plantations and nucleations) would recover vegetation structure (e.g. basal area and canopy cover) faster than natural regeneration (Holl et al. 2020) structurally resembling old-growth native forests. Successional forests would have higher species richness than old-growth native forests due to their dynamic nature and structural complexity (Lebrija-Trejos et al. 2010), and comparing successional forests after different restoration practices, natural regeneration would support higher species richness (Crouzeilles et al. 2017). Environmental factors related to the mountain moist forests at high elevations (lower temperature and precipitation and higher seasonality in temperature and precipitation) would support higher basal area and tree density but lower species richness when compared to lowland forests (Malizia et al. 2020). Basal area, tree density, and species richness would increase with succession time (Chazdon et al. 2007) and be highest after forest degradation (vs. agriculture, cattle farming, or mining) (Florentine & Westbrooke 2004).

Methods

Study Area

This study focused on moist forest, one of six Colombias biomes, as defined by Olson et al. (2001). This biome is estimated to originally cover 854.528 km^2, and due to land cover change, currently extends for 555.156 km^2, about 65% of its original area (Fig. 1). Moist forests extend across five ecoregions of Colombia (Amazonian, Pacific, Andean, Caribbean, and Orinoco), distributed along an elevation gradient ranging from sea level to 3000 m (Hofstede et al. 2014). Due to the wide distribution of moist forest in Colombia, its environmental characteristics and deforestation trends are heterogeneous (see Table S2).

In the Amazon, illegal logging, illicit crop cultivation (mainly coca), and extensive cattle ranching are the primary causes of forest loss (Agudelo-Hz et al. 2023), resulting in a 12.5% reduction in forest area (IDEAM 2023). The Pacific region faces deforestation due to illegal logging, palm oil plantations, and illegal mining (Sanchez-Cuervo & Aide 2013), contributing to a 34% loss of its original forests (IDEAM 2023). The Andean region has seen nearly 67% of its moist forests cleared, driven by large urban expansion, agricultural intensification, and mining (Vanegas-Cubillos et al. 2022). In the Caribbean,



Original Moist Forest (Olson et al. 2001)

Remmant Moist Forest 2021 (IDEAM)

Figure 1. Colombian original tropical moist forest (left, according to Olson et al. 2001) and its extension in 2021 (right, according to IDEAM 2023), with the research location of the articles analyzed in this study (purple dots).

deforestation has reached 85% of its original forest cover, mainly due to agricultural expansion, infrastructure development, and livestock grazing (Etter et al. 2006). Finally, the Orinoco region, dominated by savanna, has lost about 30% of its moist forests, largely due to cattle ranching and agriculture (Sanchez-Cuervo et al. 2012).

Literature Search and Selection Criteria

We conducted a systematic search on 3 October, 2023, without limiting the date of publication, for scientific literature in the SCOPUS, Web of Science, and Scielo databases following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol (O'Dea et al. 2021). The search strategy included five different word combinations, all incorporating the terms "Colombia AND forest." Then, variations considering different management actions were included in each string search: (1) "ecolog* AND restor*," (2) "natural regeneration," (3) "rehab*," (4) "remed*," and (5) "recov*" (Fig. 2). The search initially yielded 702 articles, which were reduced to 407 after removing duplicates. Screening based on titles and abstracts excluded 160 articles that were not research articles or did not investigate moist forests.

We screened the remaining 247 articles to identify studies on successional forests (via natural regeneration or active restoration) and old-growth native forests that reported key variables describing successional forests and factors influencing them (described in Section 2.3); our selected articles used for the meta-analyses also met the criteria of comparing nearby locations with similar succession time and prior land use activity to avoid site selection bias (sensu Reid et al. 2018). We yielded a final set of 34 articles meeting our criteria; these were located in forests in the Andean ($n = 26$; 76%), Amazon ($n = 5$; 15%), and Pacific regions ($n = 3$; 9%) (see Fig. 1). No suitable articles were found for moist forests in the Caribbean and Orinoco regions. The selected articles varied in measured variables (e.g. aerial biomass, basal area, species richness, leaf litter, and soil nutrients) and comparisons (e.g. succession after active restoration vs. natural regeneration, or both compared to old-growth native forests); therefore, to address our research questions, we grouped them into three different subsets (one to each question) based on these variations.

Data Extraction

From the 34 selected articles, data on location, succession time, prior land use activity, and restoration methods were extracted (see the descriptive metadata in Table S3). Location provided the geographic coordinates of the study sites; otherwise, these were manually determined (locations reported in Fig. 1). Succession time refers to the number of years since succession began. Prior land use activity was categorized into agriculture, cattle farming, combined agriculture/cattle farming, deforestation (clear cutting without further land use), degraded forest, gold mining, and conifer plantations (*Pinus* spp. or *Cupressus* spp.). Restoration methods included natural regeneration, native or exotic plantations, nucleation, remediation, agroforestry, or silvopastoral systems (described in Table S1).

Measured variables describing forests (secondary succession by natural regeneration or active restoration and old-growth native forest) were classified into four categories: vegetation structure (aerial biomass, basal area, canopy cover, height, and

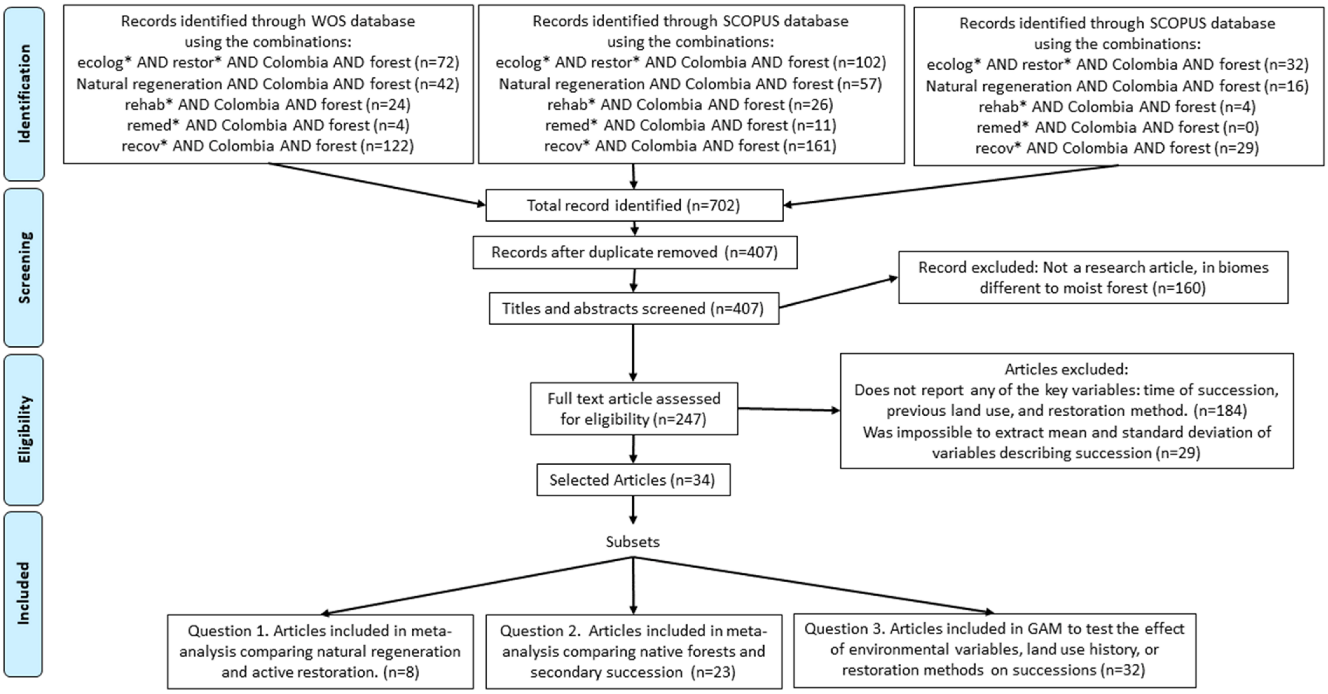


Figure 2. PRISMA flow diagram of the search and inclusion process used in this study.

tree density), leaf litter (depth and production), soil nutrients (carbon, phosphorus, and nitrogen content), and species richness (plants, frogs, and insects). Data for mean and standard deviation of variables were extracted from tables, Tables S1–S5 and Figures S1–S3, or text. When data was missing, the WebPlotDigitizer tool (that helps extract numerical data from images of a variety of data visualizations, Ankit 2022) was used to estimate values from figures. Variable units are detailed in the descriptive metadata (see Table S3). The selected articles typically included at least three variables, though these varied across studies, and some articles featured multiple cases, comparing different restoration methods or old-growth native forests to successional forests (resulting from various restoration approaches or natural regeneration) in different locations. A summary of the extracted data for each research question is available in Table S4, and the full dataset can be accessed at Zenodo: https://zenodo.org/records/14967708.

Data Analysis

To address question 1 (comparing active restoration and natural regeneration) and question 2 (comparing successional forests and old-growth native forests), we conducted separate meta-analyses for each response variable category. Using mean and standard deviation values from the selected articles, we calculated the standardized mean difference (SMD) by dividing the mean difference by the study's standard deviation. The calculation of SMD was done using the *escalc* function in the R package Metafor (Viechtbauer 2010), which corrects for positive bias in SMD (Cohen's *d*), yielding Hedges' *g* (Hedges 1981). We applied a moderator analysis, using restoration methods as moderators, within a random-effects model (to account for study heterogeneity; Borenstein et al. 2021) to compare active restoration versus natural regeneration for question 1 and to compare successional forests, under different restoration methods, with old-growth native forests for question 2.

For question 1 two meta-analyses were conducted:

(1) Vegetation structure (basal area, canopy cover, height, and tree density; $n = 16$ cases, three articles comparing exotic plantation and native plantation with natural regeneration). Succession time ranged from 30 to 50 years, with all cases located in the Andean region and prior land uses including conifer plantations, cattle farming, and combined agriculture and cattle farming.

(2) Species richness (plants, birds, and insects; $n = 13$ cases, eight articles comparing exotic plantation, native plantation, and nucleation with natural regeneration). Succession time ranged from 3 to 50 years, with only 23% of cases ($n = 3$) under 30 years. All cases were located in the Andean region, with prior land uses including gold mining, conifer plantations, cattle farming, and combined agriculture and cattle farming.

Both meta-analyses used paired data, ensuring that prior land use activity and succession time were consistent across study cases.

For question 2, four meta-analyses were conducted:

(1) Vegetation structure (aerial biomass, basal area, canopy cover, height, tree density; $n = 52$ cases, 11 articles comparing native plantation, natural regeneration, remediation, and silvopastoral system with old-growth native forest). Succession time ranged from 2 to 50 years, with 77% of cases under 30 years. Half of the cases were located in the Andean region ($n = 26$), while the other half were distributed between the Amazon ($n = 19$) and Pacific ($n = 7$). Prior land uses included deforestation, forest degradation, gold mining, cattle farming, and combined agriculture and cattle farming.

(2) Leaf litter (depth and production; $n = 9$ cases, three articles comparing exotic plantation, native plantation, and natural regeneration with old-growth native forest). Succession time ranged from 7 to 43 years, with 60% of cases ($n = 6$) under 30 years. Six cases were located in the Andean region and four in the Amazon. Prior land uses included conifer plantations and cattle farming.

(3) Soil nutrients (carbon, phosphorus, and nitrogen content; $n = 13$ cases, three articles comparing native plantation, natural regeneration, and agroforestry system with old-growth native forest). Succession time ranged from 10 to 14 years, with 1 case in the Andean region and 12 in the Amazon. Prior land use was exclusively cattle farming.

(4) Species richness (plants, frogs, and insects; $n = 8$ cases, 14 articles comparing exotic plantation, native plantation, natural regeneration, and remediation with old-growth native forest). Succession time ranged from 1 to 50 years, with 87% of cases ($n = 33$) under 30 years. Sixty percent of cases were located in the Andean region ($n = 23$), while the remaining 40% were distributed between the Amazon ($n = 12$) and Pacific ($n = 3$). Prior land uses included forest degradation, gold mining, cattle farming, and conifer plantations.

For each meta-analysis we tested the residuals heterogeneity test for residual heterogeneity (QE) (variability not explained by the moderators) and the influence of the moderator on the result joint null-hypothesis test (QM) (the variability explained by the restoration method). We also assessed the influence of individual cases in each meta-analysis using diagnostic plots: *rstudent* (model fit), *dffit* (influence on predicted values), and *weight* (contribution to the meta-analysis). Publication bias was evaluated using funnel plots and Egger's test of asymmetry (see Fig. S1).

It is important to note that other key factors influencing forest succession—such as environmental conditions, time since restoration began, and previous land use activities—were not accounted for in the meta-analyses due to insufficient data across the studies. This limitation prevented us from including these variables as explanatory factors in our analysis. To address this gap, we used the compiled data from questions 1 and 2 to answer question 3, specifically to test the influence of these variables on succession.

To address question 3, which examines the influence of environmental variables, succession time, prior land use activity, and restoration methods on response variables—tree density ($n = 68$), basal area ($n = 37$), and species richness of plants ($n = 47$), birds ($n = 8$), and insects ($n = 13$)—we used

Multivariate Generalized Additive Models (GAMs). These were implemented with the R packages mgcv (Wood 2017) and mgcViz (Fasiolo et al. 2018). Data on succession time, prior land use activity, and restoration methods were extracted from the articles, while environmental variables were obtained for each study location using the R packages raster (Hijmans 2024) and sp. (Bivand et al. 2013). Initially, 19 WorldClim variables (see Table S5; Fick & Hijmans 2017) and elevation data (ESA 2021) were extracted. To reduce redundancy, a Spearman correlation test (using hmisc; Harrell Jr 2023) and visualization (corrplot; Wei & Simko 2021) were performed (see Fig. S2). Variables showing a strong ($r > 0.65$) and statistically significant ($p < 0.05$) correlation, and deemed redundant in interpretation, were excluded from further analysis, resulting in six uncorrelated variables: BIO1 (mean annual temperature), BIO4 (temperature seasonality), BIO12 (annual precipitation), BIO14 (precipitation of the driest month), BIO15 (precipitation seasonality), and MASL (elevation). These variables capture temperature, precipitation, and altitude variability while minimizing redundancy. A principal component analysis (PCA) (factoextra; Kassambara & Mundt 2020) was applied to these six variables to further reduce dimensionality while retaining significant variation (see Fig. S3). To identify the components that were statistically meaningful and explained substantial variance, we validated the PCA results using the broken-stick method. The first two principal components (Dim1 and Dim2) accounted for more variance than expected under this model (see Fig. S3), and their scores for each study location were subsequently used as environmental predictors in the GAMs. This approach ensured that the models captured the most relevant environmental gradients while maintaining ecological interpretability.

Results

Of the 34 selected articles to address our research questions, 17 (50%) focus exclusively on natural regeneration, 11 (32%) compare natural regeneration with active restoration techniques, and the remaining six (18%) evaluate only active restoration techniques without comparison to natural regeneration.

The most frequently reported prior land use is cattle farming, mentioned in 25 studies (73.5%). The primary driver of succession is land abandonment (26.4%), followed by biodiversity conservation mentioned in eight studies (23.5%). Succession times range from 0 to 60 years, with more than half of the cases reporting successions younger than 10 years.

Comparison of Natural Regeneration With Active Restoration Methods

When comparing vegetation structure (basal area, canopy cover, height, and tree density) between actively restored and naturally regenerated forests in areas with similar succession time and prior land use activity, the overall test of moderators was significant (QM [degrees of freedom [*df*] 2] 6.45; p value = 0.04), indicating that restoration methods influenced vegetation structure. Specifically, exotic plantations showed significantly lower values on the variables related to vegetation structure (basal area, canopy cover, height, and tree density) compared to natural regeneration (SMD −0.75; SE 0.30; p value = 0.01), while native plantations did not exhibit a significant differences (SMD −0.21; SE 0.58; p value = 0.71). The model exhibited significant residual heterogeneity (I^2 76.5%; QE [*df* 14] 59.26; p value <0.01), suggesting substantial variability not explained by the moderators (Fig. 3A). Diagnostic plots revealed no influential outliers, and no significant publication bias was detected in the funnel plot (see Fig. S1a) and its Egger's test of asymmetry (t [*df* 13] −1.26; p value = 0.23).

For species richness (plants, birds, and insects), the test of moderators was not statistically significant (QM [*df* 3] 5.33; p value = 0.15), indicating that restoration methods did not strongly influence species richness. However, nucleation showed a marginally significantly higher values on species

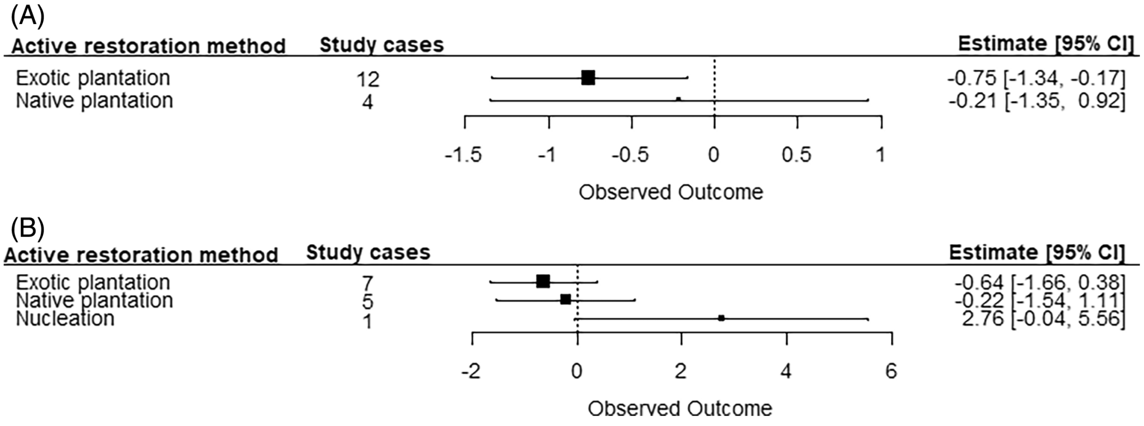


Figure 3. Standardized mean differences with its 95% CI in (A). Vegetation structure (basal area, canopy cover, height, tree density) and (B). Species richness (plants, birds, and insects) between successional forests after different active restoration methods vs. successional forests by natural regeneration. Active restoration method (exotic plantation, native plantation and nucleation) was used as a moderator in the model and is represented in each row. Negative values represent greater values for Natural regeneration. The size of the box indicates the weight of the data in the model, and the bars represent its associated standard error.

richness compared to natural regeneration (SMD 2.76; SE 1.43; p value $= 0.05$), while exotic plantations (SMD -0.63; SE 0.52; p value $= 0.22$) and native plantations (SMD -0.22; SE 0.68; p value $= 0.75$) did not exhibit significant effects. The model revealed substantial residual heterogeneity (I^2 85.12%; QE [df 10] 60.97; p value <0.01), indicating significant unexplained variability (Fig. 3B). Diagnostic plots (see Fig. S1b) identified one atypical value, but no significant publication bias was detected in the funnel plot and its Egger's test of asymmetry (t [df 9] -1.46; p value $= 0.18$).

Comparison of Old-Growth Native Forest With Successional Forests

When comparing vegetation structure in terms of aerial biomass, basal area, canopy cover, height, tree density between old-growth native forests and successional forests (after native plantation, natural regeneration, remediation, and silvopastoral system) the test of moderators was significant (QM [df 4] 18.24: p value <0.01), indicating that restoration methods influenced vegetation structure recovery. Old-growth native forests exhibited significantly higher values of vegetation structure in terms of aerial biomass, basal area, canopy cover, height, tree density than natural regeneration (SMD 3.04; SE 0.83; p value <0.01) and remediation (SMD 3.48; SE 1.74; p value $= 0.04$). No significant differences were found between old-growth native forests and native plantations (SMD 2.39; SE 5.06; p value $= 0.64$) or silvopastoral system (SMD -4.03; SE 4.99; p value $= 0.42$) (Fig. 4A). The model showed significant residual heterogeneity (I^2 98.05%; QE [df 47] 481.46; p value <0.01), indicating significant unexplained variability. Diagnostic plots revealed no influential outliers (see Fig. S1c), but significant publication bias was detected in the Egger's test (t [df 46] 6.17; p value <0.01) and the funnel plot (see Fig. S1c).

Regarding leaf litter depth and production, the test of moderators was not statistically significant (QM [df 3] 5.17; p value $= 0.16$), indicating that restoration methods did not strongly influence leaf litter. Perhaps, exotic plantation showed a significantly lower value than old-growth native forest (SMD 44.15; SE 19.61; p value $= 0.02$) while native plantation and natural regeneration had no significant differences with old-growth native forest (SMD 1.45; SE 13.31; p value $= 0.91$ for native plantation and SMD 4.09; SE 13.33; p value $= 0.76$ for natural regeneration) (Fig. 4B). The residual heterogeneity in this model is significant (I^2 100%; QE [df 7] 266.89; p value <0.01), indicating significant unexplained variability. Two outliers were identified in diagnostic plots (see Fig. S1d), and marginal publication bias was detected in the funnel plot and Egger's test (t [df 6] 2.61; p value $= 0.04$).

For soil nutrients (carbon, phosphorus, and nitrogen content) the test of moderators was not statistically significant (QM [df 3] 5.17; p value $= 0.16$), indicating that restoration methods did not strongly influence soil nutrients. No significant differences were found between old-growth native forests and any restoration method (SMD 1.29; SE 1.38; p value $= 0.35$ for agroforestry system, SMD 0.42; SE 0.18; p value $= 0.85$ for native plantation, and SMD -0.86; SE 0.78; p value $= 0.27$ for natural regeneration). The model showed significant residual heterogeneity (I^2 85.03%; QE [df 10] 52.25; p value <0.01) indicating significant unexplained variability. No outliers were detected in diagnostic plots (see Fig. S1e) neither was publication bias found in the funnel plot symmetry (see Fig. S1e) and Egger's test (t [df 9] -1.25; p value $= 0.24$).

Finally, when comparing species richness (plants, frogs, and insects) between old-growth native forests and successions with different restoration methods, the test of moderators was significant (QM [df 3] 40.83: p value <0.01), indicating that restoration methods influenced species richness. Old-growth native forests had significantly higher species richness than native plantations (SMD 2.05; SE 0.54; p value <0.01) and natural regeneration (SMD 1.50; SE 0.30; p value <0.01), but no significant differences were observed compared to remediation (SMD1.72; SE 1.31; p value $= 0.19$) (Fig. 4D). The model showed significant residual heterogeneity (I^2 81.07%; QE [df 35] 156.64; p value <0.01) indicating significant unexplained variability. Two outliers were identified in diagnostic plots

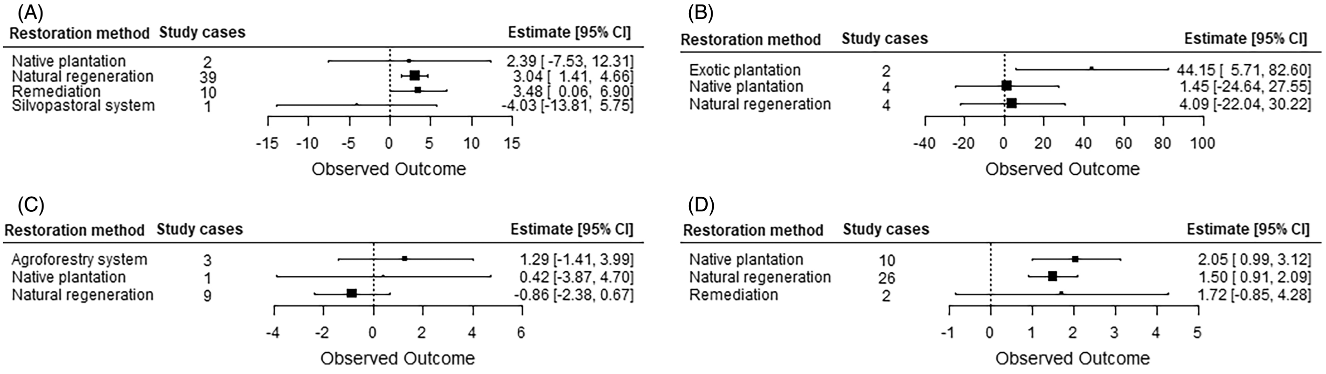


Figure 4. Standardized mean differences estimated with its 95% CI in (A). Vegetation structure (aerial biomass, basal area, canopy cover, height, and tree density), (B) leaf litter depth and production, (C) soil nutrients (carbon, phosphorus, and nitrogen content), (D) species richness (plants, frogs, and insects) between old-growth native forests versus successional forests. Restoration method (native plantation, exotic plantation, remediation, natural regeneration agroforestry systems, and silvopastoral systems) was used as a moderator in the model and is represented in each row. Negative values represent greater values for successional forests. The size of the box indicates the weight of the data in the model, and the bars represent its associated standard error.

(see Fig. S1f), and significant publication bias was detected in the Egger's test (*t* [*df* 34] 3.04; *p* value <0.01) and the funnel plot (see Fig. S1f).

Identification of Variables Influencing Successions

As a result of the PCA performed on the six chosen environmental variables (BIO1-Annual Mean Temperature, BIO4-Temperature Seasonality, BIO12-Annual Precipitation, BIO14-Precipitation of Driest Month, BIO15-Precipitation Seasonality and MASL-Elevation), the first principal component (Dim.1) explains the largest variability in the data (57%) and is strongly influenced by BIO12 (25.1%), MASL (22.7%), and BIO14 (20.8%), indicating that annual and driest month precipitation (BIO12 and BIO14) and altitude (MASL) are key drivers of variability in this dimension. The second principal component (Dim2) explained 28.7% of the variance of the data, and the main contributors for this component are BIO4 (32.8%) and BIO15 (28.0%), suggesting that temperature seasonality (BIO4) and precipitation seasonality (BIO15) play a significant role in explaining variability in Dim2 (see Fig. S3). Dim1 is positively associated with annual precipitation and driest month precipitation and negatively associated with elevation. On the other hand, Dim2 shows a negative association with both temperature seasonality and precipitation seasonality. Considering this result, Dim1 (annual and driest month precipitation; altitude) and Dim2 (seasonality in temperature and precipitation) were used as representations of the environmental variables in the multivariate GAMs analysis.

Analyzing the influence of environmental variables, succession time, prior land use activity, and restoration methods on vegetation structure (tree density and basal area) and species richness (plants, birds, and insects) in successional forests with Multivariate GAMs, we found that only tree density, basal area, and bird richness are significantly influenced by some of these variables (Table 1; Fig. 5). Tree density decreases with increasing precipitation and decreasing elevation (Dim1) (Fig. 5A) and also with decreasing seasonality in temperature and precipitation (Dim2) (Fig. 5B). Basal area increases with higher precipitation and lower elevation (Dim1) (Fig. 5B), lower seasonality (Dim2) (Fig. 5D), and over time during succession (Fig. 5E); it also varies with prior land use activity, being highest in areas affected by forest degradation and gold mining (Fig. 5F). Bird richness is higher in regions with more precipitation and lower elevation (Dim1) (Fig. 5G) and tends to decline slightly over time during ecological succession (Fig. 5H). The restoration method (natural regeneration, native or exotic plantations, and remediation) does not significantly affect vegetation structure and species richness for the studies used in this comparison (Table 1).

Discussion

Our findings provide important insights into the role of environmental drivers in advancing ecological restoration efforts, as well as the significant variability in restoration outcomes observed on the ground. Our results for question 1, comparing different active restoration methods with natural regeneration after 30 years of succession, showed that natural regeneration

Table 1. Statistical results of multivariate GAMs.

Explanatory variables		Response variables				
		Vegetation structure		Richness		
		Tree density (ind/ha)	*Basal area (t/ha)*	*Insects*	*Birds*	*Plants*
Dim1 (annual and driest month precipitation; altitude)		$F = 6.50; p < 0.01$*	$F = 25.54; p < 0.01$*	$F = 1.24; p = 0.38$	$F = 32.27; p = 0.03$*	$F = 0; p = 0.97$
Dim2 (seasonality in temperature and precipitation)		$F = 4.89; p < 0.01$*	$F = 15.69; p < 0.01$*	$F = 3.15; p = 0.15$	$F = 1.16; p = 0.47$	$F = 0.09; p = 0.76$
Succession time (years)		$F = 0.62; p = 0.43$	$F = 15.50; p < 0.01$*	$F = 0.28; p = 0.67$	$F = 45.83; p = 0.04$*	$F = 2.13; p = 0.16$
Prior land use activity	Cattle farming	$T = -0.43; p = 0.67$	$T = 6.36; p < 0.01$*	ND	ND	$T = -0.07; p = 0.94$
	Forest degradation	$T = 1.13; p = 0.26$	$T = 5.65; p < 0.01$*	ND	ND	$T = 1.17; p = 0.25$
	Gold mining	$T = -0.24; p = 0.81$	$T = 4.92; p < 0.01$*	ND	ND	$T = -0.05; p = 0.96$
	Conifer plantation	ND	ND	$T = 0.74; p = 0.50$	ND	$T = 0.14; p = 0.89$
Restoration method	Native plantation	$T = 0.38; p = 0.70$	$T = -1.18; p = 0.25$	ND	$T = 0.98; p = 0.43$	$T = -0.82; p = 0.42$
	Exotic plantation	ND	ND	ND	ND	ND
	Natural regeneration	$T = 0.63; p = 0.53$	$T = -1.92; p = 0.07$	$T = -0.35; p = 0.75$	$T = -0.06; p = 0.96$	$T = -0.98; p = 0.33$
	Remediation	$T = -0.09; p = 0.93$	$T = 0.25; p = 0.80$	ND	ND	$T = -0.22; p = 0.83$

*indicate statistical significance at $p < 0.01$.
Abbreviation: ND, no data (indicates that there were insufficient data to run the model).

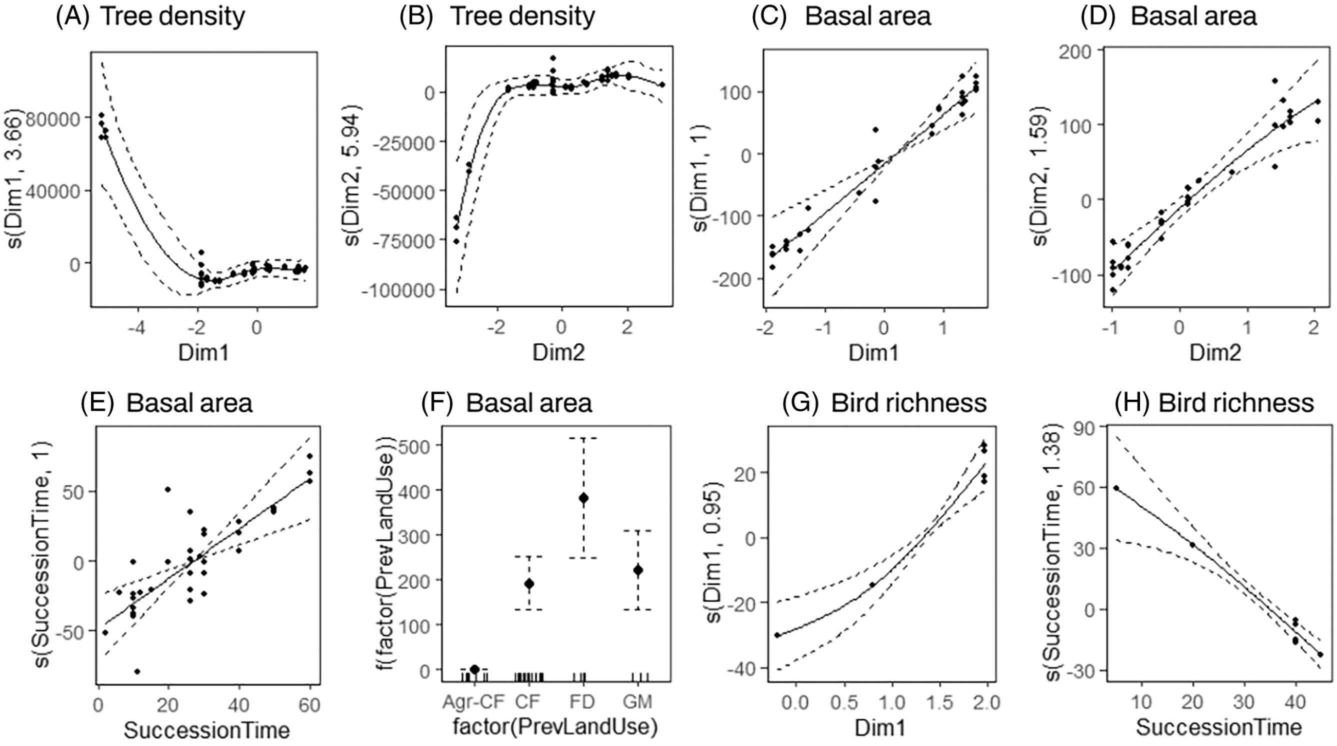


Figure 5. Results of significant multivariate generalized additive models (GAMs). Relation of Dim1 (A) and Dim2 (B) with tree density. Relation of Dim1 (C), Dim2 (D), succession time (E), and prior land use activity (F) with basal area. Relation of Dim1 (G) and Dim2 (H) with bird richness. Dashed lines represent 95% CIs, while black dots represent the observed data. Agr-CF, agriculture and cattle farming; CF, cattle farming; FD, forest degradation; GM, gold mining. Dim1: Positively associated with annual precipitation and precipitation of the driest month; negatively associated with altitude. Dim2: Negatively associated with temperature seasonality and precipitation seasonality.

leads to a vegetation structure characterized by a higher basal area, greater canopy cover and height, and greater tree density compared to exotic plantation, while compared to native plantations, there are no significant differences. This result contradicts our hypothesis that both native or exotic plantations will recover vegetation structure faster than natural regeneration. Plantations of native species are closer to natural regeneration in restoring the vegetation structure than plantations of exotic species, as they are better adapted to local conditions and facilitate natural ecological processes, such as enhancing soil fertility, supporting local fauna, and promoting the regeneration of other native species over time (César et al. 2018). In contrast, plantations of exotic species often disrupt local ecosystems, as they may outcompete native flora, alter soil properties, and provide limited habitat for native wildlife (D'antonio & Meyerson 2002). Species richness, which we expected to be greater in natural regeneration than in any active restoration method, did not show significant differences between any active restoration approach and natural regeneration. This finding underscores the resilience of tropical moist forests and their capacity to recover species diversity through different pathways (Guariguata & Ostertag 2001). Additionally, the similarity in species richness across restoration methods suggests that natural regeneration can be a cost-effective and ecologically sound strategy in areas where conditions allow it (Chazdon & Guariguata 2016), while active restoration remains a valuable tool for accelerating recovery in highly degraded or fragmented landscapes (César et al. 2018).

When evaluating question 2, which compares old-growth native forests with successional forests through different restoration methods, we found that vegetation structure—measured in terms of aerial biomass, basal area, canopy cover, height, and tree density—is significantly lower in forests restored through natural regeneration and remediation actions compared to old-growth native forests. In contrast, these metrics do not differ significantly between native plantations, silvopastoral systems, and old-growth native forests. This result supports our hypothesis and highlights the role of active restoration, particularly the planting of native trees in accelerating the successional process, especially in younger successions (less than 30 years old) (Chazdon et al. 2007). Active restoration methods, such as native plantations and silvopastoral systems, recover better vegetation structure in secondary forests and resemble old-growth native forests more than natural regeneration alone, particularly in the early stages of succession (César et al. 2018).

Leaf litter depth and production and soil nutrients (carbon, phosphorus, and nitrogen content) were not strongly influenced by restoration method and do not show significant differences when compared with old-growth native forests. This suggests that nutrient cycling processes recover equally well in actively restored and naturally regenerated forests, showing a high resilience in terms of the ecological services and functions involving both variables, supporting findings by Martin et al. (2013). A meta-analysis developed by Martin et al. (2013) demonstrated that secondary tropical forests have soil carbon content like old-growth native forests, indicating that soil carbon is either resilient to land use change or accumulates rapidly following land abandonment. However, these results should be interpreted with caution, as they are based on a reduced number of case studies. Few studies have compared soil quality and litter production between natural regeneration, active restoration (with planting trees activities) and old-growth native forests, and there is high variability in these factors (Celentano et al. 2011). Therefore, more research is needed to obtain better conclusions.

Contrary to the expectation that successional forests would have higher species richness due to their dynamic nature and structural complexity (Lebrija-Trejos et al. 2010), these results show reduced species richness in the groups studied (plants, frogs, and insects) for native plantation and natural regeneration compared with old-growth native forest. The lower species richness observed in secondary forests may be attributed to the relatively young age of most of these successions (Van Breugel et al. 2007), which are less than 30 years old, or also to the barriers in dispersion due to geographic distances from the species pool or the absence of dispersal agents, derived from forest degradation (Holl & Aide 2011).

The substantial residual heterogeneity observed in the meta-analyses underscores the inherent variability in restoration contexts, which remained unaccounted for in this study. This highlights the critical importance of adopting site-specific restoration strategies that integrate land use history and landscape context into decision-making. For instance, active restoration should be prioritized in highly degraded or fragmented landscapes, particularly those with a history of intensive land use (e.g. agriculture, cattle farming, and mining), where natural recovery capacity is compromised. Conversely, natural regeneration may be enough in ecologically resilient, well-connected regions, especially where historical land use has been less disruptive (e.g. forest degradation or recently deforested).

When evaluating question 3, our results partially support the hypothesis. We found that tree density decreases while basal area increases with increasing precipitation and lower elevation, as well as with reduced seasonality in temperature and precipitation. Bird richness is also greater in areas with more precipitation and lower elevation. These environmental conditions are mostly found in the Amazon and Pacific regions (Mesa et al. 2021), where moist forests remain among the best conserved in the country (IDEAM 2023). In these regions, secondary succession tends to be more resilient due to their strong connectivity with old-growth forests, which provide seed sources and dispersers (Pineda-Zapata et al. 2024). As expected, basal area increases over time as trees grow and forests mature (Chazdon et al. 2007). Although climate change is not directly addressed in our study, the influence of climatic variables on forest structure and biodiversity suggests that shifts in precipitation and temperature patterns could significantly impact recovery processes, particularly in regions currently favored by stable and humid conditions.

The activity of land use prior to succession also plays an important role in shaping vegetation structure, particularly basal area. Recovery of basal area following forest degradation without further land use is generally greater than lands previously used for agriculture or cattle farming. This result obeys different phenomena. Lands cleared for agricultural purposes or grazing may undergo more severe soil degradation or alteration, thereby hindering the recovery of forest structure (Florentine & Westbrooke 2004) or that loss of connectivity between deforested lands and remnant habitat patches hinders seed dispersal and seedling recruitment, slowing the succession process (Arroyo-Rodríguez et al. 2017).

Bird richness decreases as succession time progresses, indicating that younger successional stages provide more diverse habitats and resources for birds, while older forests may have more homogeneous structures and fewer niches (Walther 2002; Chazdon et al. 2007; Lebrija-Trejos et al. 2010). This greater number of habitats in younger successional stages may be easily explained by the classic intermediate disturbance theory (Connell 1978), arguing that high diversity is maintained only in a non-equilibrium state.

The restoration method (native plantations, exotic plantations, natural regeneration, and remediation) did not significantly influence vegetation structure or species richness in the studies included in this comparison. This result is likely due to the greater impact of environmental variables, represented by annual and driest month precipitation and altitude and seasonality in temperature and precipitation in the multivariate GAM models. Moreover, since most studies used in these analyses focused on natural regeneration, while other restoration methods were underrepresented, the full variability of the data is not captured. Therefore, this finding is not conclusive, and further research with more comprehensive data on all restoration methods across different locations in the Colombian Moist Forest is necessary to obtain more accurate conclusions. We acknowledge as a limitation of our research to answer question 3 the evaluation of only a selected set of explanatory variables (annual and driest month precipitation, altitude, temperature and precipitation seasonality, succession time, prior land use activity, and restoration method). While we prioritized those variables that we considered most influential, the high heterogeneity of our dataset—spanning three regions of the country—means that other important explanatory variables may have been overlooked.

In Colombia, ecological restoration efforts are primarily concentrated in the Andean region. This focus is largely driven by the need to conserve and regulate water sources for the country's major cities, which are home to 70% of the national population and serve as hubs of political and economic activity (DANE 2005; Murcia & Guariguata 2014). The extensive loss of moist forest in the Andes—where only 33% of the original cover remains (IDEAM 2023)—combined with the urgent need to secure water resources for urban and agricultural use (Garibello et al. 2021), and the concentration of research centers and major universities in Andean cities such as Bogotá, Cali, and Medellín, likely explains the high number of restoration studies identified in this review (23 studies). The Amazon region follows with 12 studies—a relatively low number given its vast area and extraordinary biodiversity. The Pacific region is also underrepresented, with only three studies. No studies meeting our criteria were found for the Orinoco and Caribbean Moist Forests, possibly due to their limited spatial extent in regions where research has traditionally focused on more dominant ecosystems, such as the Orinoco savannas (Romero-Ruiz et al. 2012) and the Caribbean dry forests (Pizano et al. 2015).

Our findings have significant implications for restoration efforts in Colombian Moist Forests, particularly in regions like the Amazon and Pacific, where high precipitation and low elevation favor faster recovery of vegetation structure and species richness. Native plantations and silvopastoral systems are particularly effective in younger successions, accelerating the recovery of vegetation structure. However, natural regeneration remains a cost-effective strategy for long-term restoration, especially in resilient areas with high connectivity to old-growth native forests. Restoration strategies should be tailored to local environmental conditions, including precipitation, elevation, and prior land use, to maximize their effectiveness. Our study highlights the importance of long-term monitoring and adaptive management to ensure the success of restoration initiatives in Colombia's Moist Forests.

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Supporting Information

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

Table S1. Restoration methods and their definitions.

Table S2. Environmental characteristics, moist forest extension, and deforestation drivers in each region.

Table S3. Descriptive Metadata for the information extracted from each research article used in this work.

Table S4. Summary of the information extracted from each research article.

Table S5. Full list of WorldClim variables extracted.

Figure S1. Diagnostic and funnel plots for the meta-analyses conducted for questions 1 and 2 of this study.

Figure S2. Spearman correlation matrix showing pairwise correlations between 19 WorldClim bioclimatic variables (BIO1 to BIO19) and elevation (MASL).

Figure S3. Projection of research locations (black dots) onto the first two principal components (Dim1 and Dim2) derived from the PCA.

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