Received: 24 November 2023 | Revised: 3 April 2024 | Accepted: 24 April 2024

DOI: 10.1111/avsc.12784

Applied Vegetation Science IAVS

RESEARCH ARTICLE

Land use legacies affect early tropical forest succession in Mexico

Iris Hordijk[1] | Lourens Poorter[1] | Miguel Martínez-Ramos[2] | Frans Bongers[1] | Rey David López Mendoza[3,4] | Pascual Jamangapé Romero[2,5] | Masha van der Sande[1] | Rodrigo Muñoz[1] | Robyn Jansma[1] | Natsuho Fujisawa[6] | Jorge A. Meave[3]

[1]Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands

[2]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico

[3]Departamento de Ecología y Recursos Naturales, Universidad Nacional Autónoma de México, México, Mexico

[4]Ejido Mena Nizanda, Asunción Ixtaltepec, Oaxaca, Mexico

[5]Ejido Loma Bonita, Ocosingo, Chiapas, Mexico

[6]Forest and Nature Conservation Policy Group, Wageningen University, Wageningen, The Netherlands

Correspondence

Iris Hordijk, Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, Wageningen, 6700 AA, The Netherlands.
Email: irishordijk@hotmail.com

Funding information

European Research Council

Co-ordinating Editor: Regina Lindborg.

Abstract

Questions: Agricultural expansion is one of the dominant drivers of forest and biodiversity loss, and shifting cultivation is the most widely used form of agriculture in many tropical forest regions. Where forests have been cleared, they have the potential to recover once the land is abandoned. However, legacies of land use are often overlooked in successional studies, and a deeper understanding of this legacy effect is needed to define efficient restoration practices using natural or assisted regeneration. Here, we analysed how land-use history affects soil properties and early succession on abandoned agricultural fields in two contrasting Mexican socio-ecological systems.

Location: Mexico, Oaxaca and Chiapas.

Methods: We sampled soil and monitored vegetation for 2 years after agricultural abandonment, and interviewed landowners about their land-use practices.

Results: Land-use practices were clearly influenced by landowners' social context (residence time, rural or urban origin), and topography and soil type also constrained or facilitated land-use practices. Soil characteristics were strongly affected by three land-use practices: mechanical tillage decreased soil N and K; frequent herbicide and pesticide use increased N and K; and for pasture systems, stocking density increased soil bulk density and decreased pH and N. High-intensity land management practices, specifically use of machinery, had the highest impact on early forest succession. When machinery was not used, the frequency of land-use practices, particularly weeding frequency, is the main factor influencing tree cover and sapling diversity.

Conclusions: To facilitate post-agricultural forest recovery, we recommend restoration efforts using natural regeneration in areas with low previous land-use intensity and frequency.

KEYWORDS

dry tropical forest, forest recovery, forest restoration, land-use history, natural regeneration, secondary succession, socio-ecological system, soil properties, topography, tropical rainforest

1 | INTRODUCTION

Land-use change is the main cause of biodiversity loss and overall forest decline in this era of mass extinction (Ceballos et al., 2015; Curtis et al., 2018). Agricultural expansion is the dominant driver of land-use change, with more than 30% of the terrestrial land surface currently allocated to agriculture (Bongaarts, 2019). In particular, tropical forests harbour high biodiversity and provide important ecosystem services, but are deforested for agricultural expansion at an alarming rate (Brockerhoff et al., 2017; FAO, 2020; Hoang & Kanemoto, 2021). In many tropical regions, shifting cultivation, a system where land is cultivated and afterwards abandoned, is the prevailing form of low-intensity subsistence agriculture (Heinimann et al., 2017). Where forests have been cleared, they have the potential to regrow as secondary forests and provide ecosystem services once the agricultural land is abandoned (Chazdon, 2014; Nanni et al., 2019). Forest regrowth can be viewed, on the one hand, as the consequence of the social system, because the local socio-economic and cultural context affects land-use practices and leaves a legacy on vegetation recovery, and as the consequence of the ecological system on the other hand, such as the proximity to seed sources (Balvanera et al., 2021; Hordijk et al., 2023; Poorter et al., 2024). To predict the recovery potential and define efficient restoration practices across different land uses and forest types, it is vital to understand the legacies of land-use history on natural forest recovery (Derroire et al., 2016). To predict the speed and direction of forest succession, focusing on the first years of this process after land abandonment is crucial, because this is the time when the successional pathway is determined and recovery rates are fast (Jakovac et al., 2021; Poorter et al., 2021). Therefore, in this study, we analyse how land-use history affects soil properties and early forest recovery after land abandonment in two tropical rural communities with different land-use practices.

Land-use practices are a result of the ecological environment, such as soil type and topography, and the social context, including traditions, social norms and values (Meyfroidt, 2013). Agricultural fields, for example, are generally established on fertile soils, particularly in flat, alluvial areas (Siebe et al., 1996; Iskandar et al., 2018). Also, soil type influences the decision to plant a certain crop and the associated management practices (Seo & Mendelsohn, 2008). In turn, land-use practices can affect soil properties, such as bulk density or fertility. For example, a high density of cattle in an area can increase soil compaction and bulk density, thus reducing water infiltration rate (Martínez & Zinck, 2004; Geissen et al., 2009). Soil compaction can have a negative effect on the establishment, growth or survival of trees, because it hinders root growth and increases erosion due to water run-off (Rauzi & Hanson, 1966; Martínez & Zinck, 2004). Soil fertility generally declines during land-use because of: (a) nutrient volatilization, especially when the fields are burned; (b) nutrient leaching when vegetation cover is sparse; or (c) removing of nutrients stocked in plants through cattle grazing and crop harvesting (Certini, 2005; Styger et al., 2007; Runyan et al., 2012; Van Der Sande et al., 2023). Farmers may mitigate nutrient losses and/or increase agricultural productivity through fertilization (to increase soil nutrient availability) or through liming (to increase soil pH) (Geissen et al., 2009). Because land-use practices modify soil properties, they may have legacy effects on the vegetation recovery after land abandonment, because reduced soil fertility is associated with slower forest regrowth, lower tree species richness, and an altered composition of woody species towards species which can resprout (Jakovac et al., 2016; Villa et al., 2018).

The starting point of vegetation recovery after agricultural land abandonment is mainly determined by the extent, duration, intensity and frequency of previous land-use practices (Jakovac et al., 2021). Vegetation recovery is facilitated by succession, which is the process of vegetation change, where increasingly taller life forms replace each other, from a by grass- and herb-dominated stage towards a shrub-dominated stage and finally a tree-dominated stage (Clements, 1916). The speed of transition between these stages of vegetation development is initially determined by propagule limitation (the availability of a seed source or resprouting capacity of the species), and secondly by establishment limitation (the opportunity to establish and grow) (Pickett et al., 1987). Land-use practices, such as slash-and-burn agriculture, degrade the viable seed bank by removing seed sources and damaging available seeds, which favour resprouting species (Chazdon, 2003; Jakovac et al., 2015). In the case of pastures, the presence of (planted) grasses makes it harder for tree seedlings to establish because of increased competition for space, water, nutrients and light (Holl, 1998; Del Castillo & Blanco-Macías, 2007). The presence of cattle also affects the regeneration of palms and woody plants, because cows browse and trample seedlings (Griscom et al., 2009; Hordijk et al., 2019). Previous land use affects not only the density, but also the diversity of tree species in early succession, by increasing the dominance of a few fast-growing, disturbance-tolerant species that are adapted to the legacies of intense land use (Zermeño-Hernández et al., 2015; Jakovac et al., 2016; Martínez-Ramos et al., 2016). Conversely, other land-use practices may facilitate the transition towards a tree-dominated stage, such as tree planting or by tending desired tree species that have established naturally (Lohbeck et al., 2020). These trees can serve as nucleation sources, through direct seed inflow or facilitating the establishment of other species (Yarranton & Morrison, 1974; Guevara et al., 1992; Holl et al., 2020).

Here, we analyse the relationships between soil type and topography, soil properties, land-use practices and early vegetation recovery after land abandonment for two rural communities with contrasting land-use practices and climatic environment (dry and wet tropical forest) in Mexico. We addressed the following research questions (Figure 1): (1) What are the different land-use practices and how are these influenced by landowner characteristics (e.g. residence time, rural or urban origin); (2a) How do soil type and topography influence land-use history and soil properties (e.g. bulk density and soil fertility), and (2b) what is the relationship between land-use history and soil properties; and (3) How do land-use history, topography and soil properties affect vegetation cover and tree diversity during early forest recovery? We hypothesize that: (1) landowners with different backgrounds use different land-use practices and (2a) local topography and soil type determine

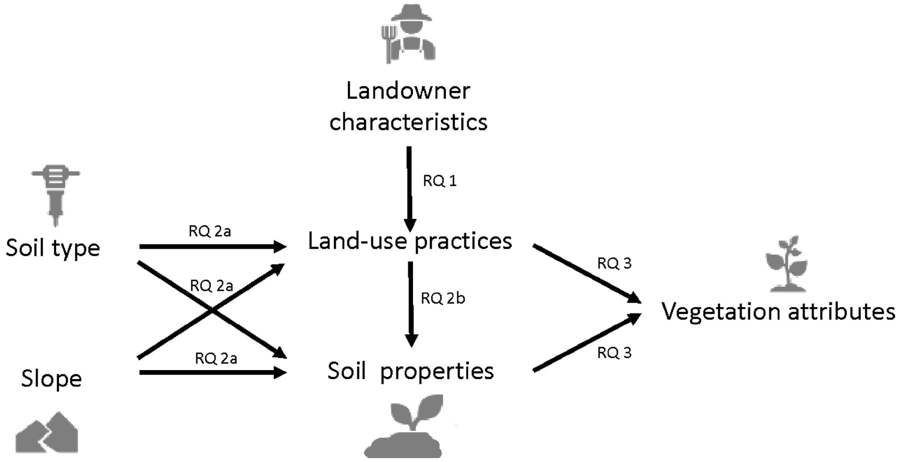

FIGURE 1 Conceptual model, showing the hypothesized cause–effect relationships (depicted by arrows) between different variables and vegetation attributes. The corresponding research questions are shown next to the arrow.

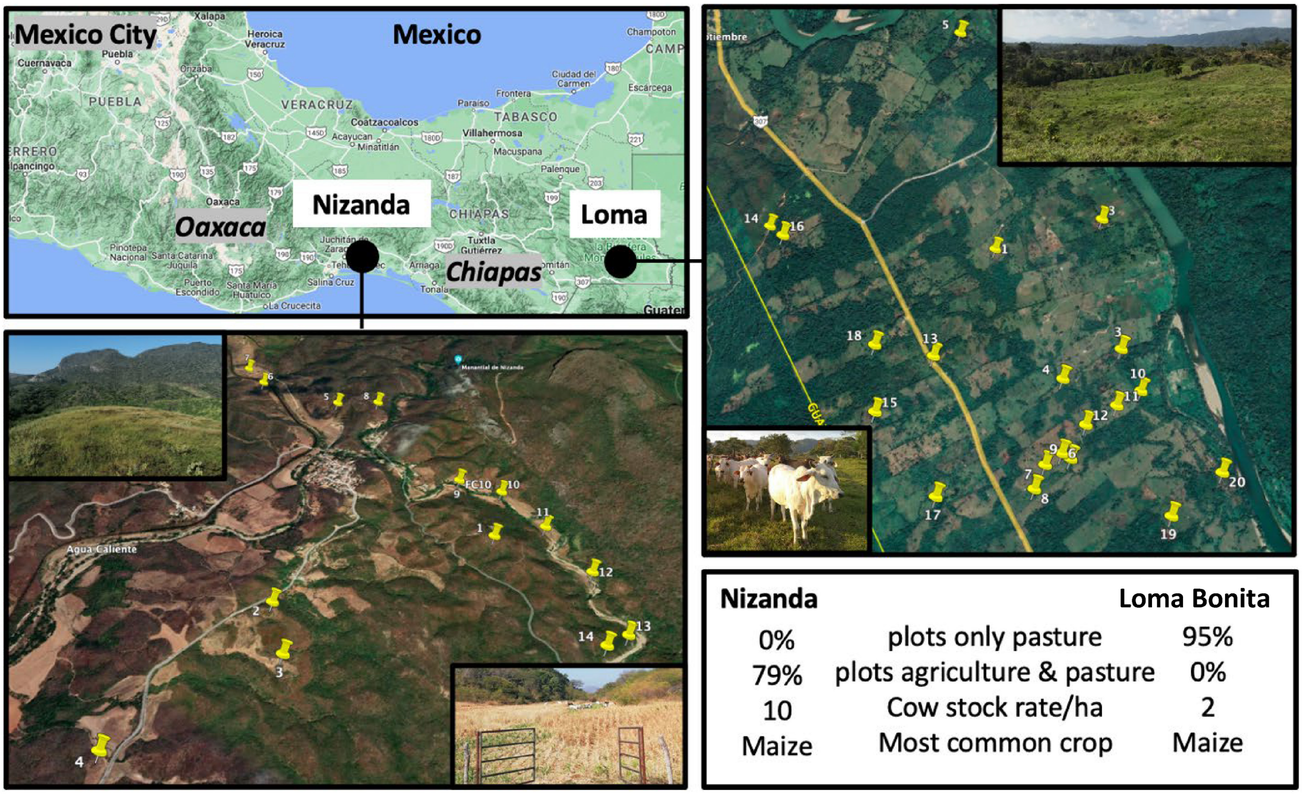

FIGURE 2 Map with locations of the sites (Nizanda, Loma Bonita) and the plots, including a description of the commonness and intensity of previous land-use practices. Picture credits: Iris Hordijk.

previous land use as they relate to local abiotic constraints. In addition, we hypothesize that a longer duration, intensity and frequency of previous land-use practices (e.g. high fire frequency, use of heavy machinery or high stocking density) (2b) increases soil compaction and degradation, as nutrients have been removed and soil has been compacted by machines and cattle, and (3) decreases tree cover and sapling diversity as woody plants were removed and a higher grass cover inhibits woody plant establishment.

2 | METHODS

2.1 | Study plots

Fieldwork was conducted in two rural communities of southern Mexico. Nizanda is located in a dry tropical forest region in Oaxaca, and Loma Bonita is located in a wet tropical forest region in Chiapas (Figure 2).

2.1.1 | Nizanda

Nizanda (16°39′ N, 95°00′ W) is located at an elevation of 90–120 m a.s.l. on the Pacific watershed of the Isthmus of Tehuantepec. Mean annual temperature is 27.7°C, with a mean annual precipitation of 900 mm (Muñoz et al., 2023). Rainfall is highly seasonal, with 90% of the rainfall occurring between late May and mid-October. In the region around Nizanda, the dominant soil types are lithosols, haplic phaeozems and eutric regosols with mainly limestone and siliciclastic and vulcanoclastic phyllite underneath (Guadarrama-Chávez et al., 2007; Pérez-García et al., 2010). The forest is classified as a tropical dry deciduous forest, typically with a canopy height of 7–8 m (Rzedowski 1978; Pérez-García et al., 2010).

With the construction of the Trans-Isthmic Railway in 1880, the population in the Isthmus of Tehuantepec increased after the founding of several towns along the railway line (Reina, 1991). The fast transformation of mature forest to agricultural lands mainly increased in the region around 100 years later (1986). Cattle ranching has shifted from traditional free-ranging to semi-intensive ranching, confining cattle within fenced areas and using high-yield exotic grass species. Traditionally, part of these human-modified lands is abandoned after agricultural use and left to recover into secondary vegetation (Gallardo-Cruz et al., 2012), which is a common shifting cultivation practice consisting of alternating agricultural periods and fallow periods to let the land recover. The main crop cultivated in the region is maize (Lebrija-Trejos et al., 2008), which is traditionally cultivated by slashing and burning the natural vegetation and subsequently sowing manually, mostly without the use of fertilizers (Guadarrama-Chávez et al., 2007). The majority of residents in Nizanda are originally from within the region and identify themselves as members of the Zapotec ethnic group.

2.1.2 | Loma Bonita

Loma Bonita (16°05′ N, 91°00′ W) is located at an elevation of 115–300 m a.s.l. in the eastern region of Chiapas, bordering Guatemala. Mean annual temperature is 24.4°C, with a mean annual precipitation of 3,000 mm. There is a relative dry season from February to April (<100 mm/month) that accounts for less than 10% of the total annual rainfall. The dominant soil types in this region are entisols and ultisols, stretching from the river edge to inland hills (Fragoso & Lavelle, 1987). The forest is classified as lowland tropical rain forest and semi-deciduous forest (Rzedowski, 1978).

Settlement in the region was encouraged by the Mexican government in the late 1970s to create a populated border zone with neighbouring Guatemala at a time when the region was sparsely populated (Berget et al., 2021). Therefore, most residents in Loma Bonita nowadays are descendants from or are themselves originally from another place in Chiapas or a different state in Mexico. The daily language in Loma Bonita is Spanish. Mature forests have been replaced by agricultural fields and pasture from the time of settlement onwards, especially during the 1980–1990s with the help of Guatemalan refugees escaping the civil war in their country. The main crops cultivated are corn and bean, and agricultural practices do not include the use of machinery. Exotic grasses are often sown in the pastures, leading to a dense grass cover (Zermeño-Hernández et al., 2016).

2.2 | Data collection

2.2.1 | Plot establishment

In total, thirty-four 25 m × 25 m plots were established in 2020: 14 in Nizanda and 20 in Loma Bonita (Figure 2). These plots were established on recently abandoned pastures or agricultural fields (0–10 months after agricultural abandonment) and their average slope was recorded in categories (0%, 1%–10%, 11%–20%, 21%–30% or 31%–40%). All plots were located within a radius of 1.5 km in Nizanda and 2.5 km in Loma Bonita. Some plots were fenced to prevent cattle from entering and browsing.

2.2.2 | Vegetation sampling

To estimate the contribution of different growth forms to vegetation structure (grasses, herbs, climbers, palms, trees), a point intersection method was conducted (Ellenberg & Mueller-Dombois, 1974). A 2-m-tall stick was placed every 1 m along two 25-m lines (Appendix S1) and all plants encountered at each 1 m were identified to species level (when possible) and classified by growth form; on average, 95% of individuals were identified at least to genus level (Appendix S2).

To quantify the regeneration of tree species, saplings were measured in four 25 m × 1 m transects (Appendix S1). In these transects, all trees <1 cm stem diameter at 30 cm height were measured for height and diameter at 30 cm, tagged and identified to species level. In addition, the larger trees ≥1 cm stem diameter at 30 cm height were measured, tagged and identified to species level in the entire plot. In Nizanda, vegetation and saplings were measured at the end of the wet season to facilitate identification (September–October), because trees are mostly leafless in the dry season. In Loma Bonita, vegetation and saplings were measured during the dry season (March–April). The vegetation and saplings were measured two years after land abandonment.

2.2.3 | Soil sampling and analysis

In Nizanda, three soil samples (0–15 cm) per plot were collected in 2020, and in case of high stone content within the soil, five samples were taken per plot. In Loma Bonita, three soil samples per plot were taken in 2022 (for the plot sampling design, see Appendix S1). Soil samples were pooled per plot and analysed at the Laboratorio de Fertilidad de Suelos y Química Ambiental at the Colegio de Postgraduados in Montecillo, Mexico. Soils were analysed on texture, organic matter content (OM), electrical conductivity (EC), pH, available nitrogen (N) with the Kjeldahl method, available phosphorus (P) with the Olsen extraction method, base cations calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}) and sodium (Na^{+}), and metals iron (Fe), copper (Cu), zinc (Zn) and manganese (Mn). In Nizanda, soil samples for bulk density were taken with a 100 cm^3 soil ring from a 5–10 cm depth following the same locations as the other soil samples (Appendix S1). In Loma Bonita, the soil contains fewer stones and bulk density is less variable, therefore a single bulk density sample was taken per plot. To calculate bulk density, the soil without stones was oven dried for 2–5 days at 105°C until a stable weight was reached. The dried soil samples were weighed with a precision of at least 0.1 g, divided by the volume of the ring and expressed in g/cm^3. For Nizanda, the mean bulk density values for the 5–10 cm depth was calculated.

Soil types were classified according to FAO's soil classification (Celedón Muñiz, 2006; IUSS Working Group WRB, 2012). In Nizanda, the plots were located on four soil types: leptosols (four plots), occur in regions where soil formation is limited by severe climatic conditions, but are used for agriculture or grazing in the wet season; regosols (five plots), soils on unconsolidated mineral material with a low water-holding capacity, used for extensive cattle grazing; fluvisols (four plots), found close to water streams and composed of alluvial deposits, fertile soils highly suitable for agriculture; and cambisols (one plot), characterized by a moderate weathering of the parental material, and used intensively for agriculture (ISRIC World Soil Information, 2023). In Loma Bonita, the plots were located on two soil types: eutric cambisols (3 plots) and dystric cambisols (17 plots). Eutric cambisols are common in hilly terrain and are more fertile than dystric cambisols (ISRIC World Soil Information, 2023).

2.2.4 | Land-use history

In Nizanda, plots were established in fields representing two main previous land uses: agriculture (3 plots) and agriculture and cattle grazing combined (11 plots). In Loma Bonita, the 20 plots were established on former pastures. The land-use history of each plot was further documented through semi-structured interviews with the local landowners or managers. Questions included, among other things, general information about the landowner, characteristics of the abandoned fields, the land-use duration and various potentially applied management practices and their frequencies (see Appendix S2 for an overview of the interview questions). In total, 32 variables were extracted from the interviews. Land-use practices that showed no or little variation within a site (none or only one plot with a different value; for example, land-use type in Loma Bonita) were removed from further analyses. For both sites, 24 variables were selected and categorized in the following six categories: (a) landowner characteristics and opinions, (b) extent and duration, (c) intensity related to agriculture, (d) intensity related to cattle grazing, (e) frequency and (f) management (see Appendix S2 for a description of the variables).

2.3 | Statistical analyses

All statistical analyses were performed for Nizanda and Loma Bonita separately because settlement history, land-use practices and forest ecosystems are very distinct between the two sites.

2.3.1 | Land-use practices

To evaluate how land-use practices were related to each other, and which combinations of practices can be identified, we performed a cluster analysis based on squared Spearman correlations between variables (Appendix S1). In addition, a principal components analysis (PCA) was performed to visualize how land-use practices were associated. To evaluate the significance of the relationships between land-use practices and landowner characteristics, because we do not consider landowner characteristics in our linear models, we used either a Pearson correlation, Spearman correlation, *t*-test, Wilcoxon test or analysis of variance (ANOVA) with HSD Tukey post-hoc test. The type of test depends on the type and distribution of the data, including normality and the homogeneity of variances.

2.3.2 | Soil and land use

To evaluate how soil type and topography affect land-use practices and soil properties we used, depending on the data type and distribution, either a *t*-test, Wilcoxon test, Fisher test or ANOVA with HSD Tukey post-hoc test.

The effect of land-use practices on soil properties were analysed through linear regression models, with land-use practices as independent variables. The land-use practice variables were scaled to facilitate comparison of relative importance of variables within and between models. Linear regression models were used to evaluate the relationships because a linear relationship between the dependent and independent variables was expected, and the model assumptions were met. Six to eight land-use variables were selected based on the above-described cluster analysis and prior grouping (Sections 2.4.1 and 2.3.1). From each cluster and group a variable was chosen based on the highest eigenvalues as these variables represent the most variation in the land-use practices. Landowner characteristics and opinions were not considered, because we assume that landowner characteristics affect land-use practices, but not soil or vegetation attributes directly. Subsequently, linear model assumptions were tested and variables causing high multicollinearity (variable inflation factor [VIF] >5) were removed. The VIF describes the multicollinearity in the independent variables of the model; higher VIF values indicate a stronger multicollinearity between variables (Kim, 2019). For Nizanda, this resulted in six land-use variables: field size (ha), total duration of land use (years), herbicide/pesticide use frequency (number/year), tillage type (with use of a stake, yoke or mechanical), tractor use (yes/no) and stocking density (cows/ha). For Loma Bonita, this resulted in eight land-use variables: total duration of land use (years), herbicide/pesticide use frequency (number/year), trees planted (yes/no), exotic grasses sown (yes/no), weeding frequency (number/year), fire events (total number), stocking density (cows/ha) and total duration of cattle grazes in the field (month/year) (Appendix S2).

To select the most influential land-use variables per soil property, a dredge model selection was performed on a linear regression model with all possible subsets and combinations of independent variables. Model selection was based on the lowest sample-corrected Akaike information criterion (AICc). Models differing <2 AICc from the best model were considered to have an equally good fit. To finally converge in a single model per soil variable, the conditional averages of the β-coefficients and p-values were calculated from these subsets of best fit models where the variable appears.

2.3.3 | Effects of soil and land-use practices on vegetation

Because of the limited number of plots and many potentially important independent variables, first linear models between soil characteristics and vegetation variables were fitted. Second, the three most important soil variables were included in the linear models when evaluating the relationship between land-use practices and vegetation variables. Third, a path model was constructed based on the significant relationships of the linear models, to identify the direct and indirect relationships between soil type and topography, soil properties and land use on vegetation cover, sapling density and diversity.

Vegetation cover was calculated as the number of hits (the number of individual plant contacts in the point intersection method) per life form divided by the total number of hits along the transects. The number of transect points without vegetation cover were included in the count of the total number of hits to have an estimate of the openness in the plot. Sapling density was calculated as the number of individuals (<1 cm DBH) per plot and richness was estimated as the number of species per plot. Evenness was calculated as standardized Hill's evenness per plot, expressed as $^{1}D-1/S-1$, where ^{1}D is the exponential Shannon diversity and S is the absolute species richness (Chao & Ricotta, 2019).

To evaluate how vegetation attributes depend on soil properties, linear models with soil properties as independent variables were fitted (Appendix S2). Three soil variables with the most significant relationships between soil and vegetation (OM, pH and K) were selected for constructing the integrated linear model. This integrated linear model evaluates how vegetation attributes are shaped by both soil properties and land-use practices. To select the most influential independent variables, a dredge model selection was performed as described above (Section 2.3.2). An overview of the best model subsets and resulting averaged models can be found in Appendix S2.

We used a partial least squares path model to identify direct and indirect cause–effect relationships between drivers and response variables. A path model analysis is composed of multiple sequential predefined relationships between a set of variables, with the assumption that the relationships are linear. The path models were constructed based on significant relationships within the linear models, and with tree cover, sapling density, richness or diversity as the ultimate dependent variables.

All analyses were performed using the R-Studio interface to R (R Core Team, R Foundation for Statistical computing, Vienna, AT) using the following packages: *car* for the linear models, *MuMIn* ("dredge" function) for automated model selection (R version 1.6; R Core Team, R Foundation for Statistical computing, Vienna, AT), *AICcmodavg* ("model.avg" function) (Mazerolle, 2023) for model subset averaging and the *plspm* package to construct the path model (Sanchez, 2013).

3 | RESULTS

3.1 | Landowners' characteristics and land-use practices

In Nizanda, fields were used for agriculture during one part of the year, and after crop harvest they were devoted to cattle grazing. The most common crop was maize (Figure 2). When evaluating land-use practices and landowner characteristics, the first PCA axis describes characteristics of the agricultural plot, such as field size and soil quality as indicated by the landowner. The second axis describes the characteristics of the landowner, expressed as previous residence (rural or urban) and years of residence in the community (Figure 3). According to the cluster analysis (Appendix S1), years of residence was positively associated with fertilizer use (Pearson correlation, $r=0.72$, $p<0.01$) and previous residence (i.e. landowners from urban origin) was associated with a higher cattle number (Tukey HSD, $p=0.02$), weeding frequency and ($p>0.05$) and a larger field size ($p>0.05$).

For Loma Bonita, the studied fields were exclusively used for cattle grazing in recent years, and the average stocking density was two cows per hectare (Figure 2). The first axis of the PCA describes plot characteristics such as field size, and the second axis describes weeding practices such as weeding type and weeding frequency (Figure 3). Field size increased with years of residence (Pearson correlation, $r=0.63$, $p<0.01$) and was larger for landowners previously living in an urban environment (t-test, $p<0.01$), whereas herbicide use decreased with years of residence in Loma Bonita (Wilcoxon test, $p=0.03$). In addition, the cluster analysis indicated that landowners that lived longer in Loma Bonita had previously lived in an urban environment (Wilcoxon test, $p=0.03$) and used their fields for

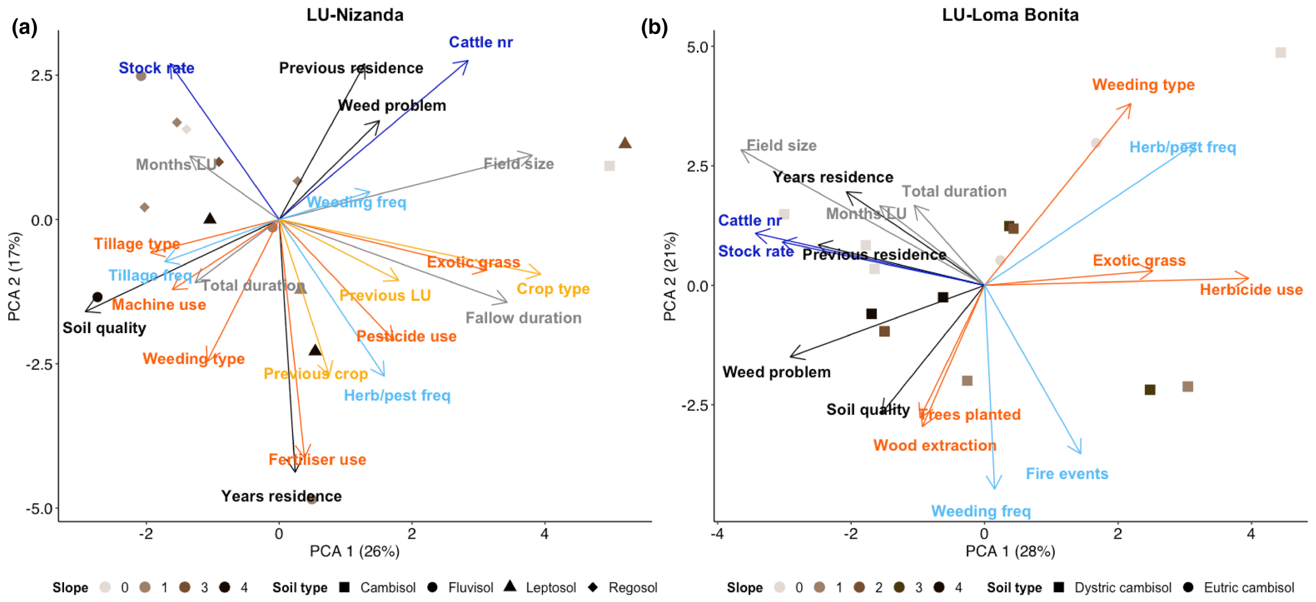

FIGURE 3 Principal components analysis (PCA) of the management practices and characteristics of the landowners in Nizanda (a) and Loma Bonita (b). The plots are indicated in the PCA, the colour corresponds to the soil type (eutric and dystric cambisols, fluvisols, leptosols and regosols) and shape to the slope steepness (0 = flat, 1 = 1%–10%, 2 = 11%–20%, 3 = 21%–30%, 4 = 31%–40%). Land-use variables have been categorized into six categories: owner characteristics and opinions (black), extent and duration (grey), intensity related to cattle grazing (dark blue), intensity related to agricultural practices (dark orange), frequency (light blue) or management (yellow). Soil quality, as indicated by the landowners in Nizanda is associated with a lower Fe concentration (*t*-test, $p = 0.05$), and in Loma Bonita with a higher soil pH and P, Ca and Cu concentrations (*t*-tests, in all cases $p \leq 0.01$). For variable explanations see Appendix S2.

a longer part of the year for grazing (Pearson correlation, $r = 0.62$, $p < 0.01$).

3.2 | Soil, topography and land-use

Soil type and topography affected soil properties and land-use practices, whereas land use affected soil properties in both communities. In Nizanda, the four soil types differed only in soil EC, because leptosols and cambisols had a higher EC compared with fluvisols and regosols (Tukey HSD, $p < 0.05$). Generally, on clayey soils there was more use of herbicides (*t*-test, $p = 0.04$), a higher frequency of herbicide/pesticide use (Spearman correlation, $r_S = -0.55$, $p = 0.05$) and weeding (Spearman correlation, $r_S = 0.56$, $p = 0.049$). Regarding topography, there was less mechanical tillage on steeper slopes (Tukey HSD, $p = 0.02$). Land-use practices that affected soil properties, and particularly soil nutrients, the most were tillage type and the frequency of herbicide/pesticide use (Table 1).

In Loma Bonita, dystric cambisols had different properties from eutric cambisols. They were located further away from the river on sandier terrain (*t*-test, $p = 0.03$), had higher soil pH (*t*-test, $p < 0.01$) and Cu concentration (*t*-test, $p = 0.02$) compared with eutric cambisols. Also, the land was used for a shorter period and showed more frequent changes in ownership (Wilcoxon test, $p = 0.03$), was less intensively used for pasture (*t*-test, $p < 0.01$), and experienced a higher fire frequency (*t*-test, $p < 0.01$). Generally, higher sand content was associated with less herbicide use (*t*-test, $p < 0.01$) and steeper slopes were associated with a higher weeding frequency (Tukey HSD, $p = 0.03$). When evaluating the effect of land-use practices on soil characteristics, stocking density has the largest effect on a wide range of soil properties (Table 1).

3.3 | The effect of topography, soil and land-use practices on early succession

Soil properties and previous land-use practices shaped, in turn, the nature and direction of the first 2 years of succession in abandoned fields (Table 2). In Nizanda, soil properties did not directly affect vegetation cover, but soil K content did increase sapling richness (linear model, $b = 0.40$, $p = 0.01$) (Table 2). Previous land-use practices did not significantly affect grass, herb or shrub cover, but had a significant effect on trees. Tractor use decreased tree cover ($b = -1.50$, $p = 0.04$) and sapling richness ($b = -1.12$, $p < 0.01$), but increased sapling evenness ($b = 0.47$, $p < 0.01$). Field size was associated with increased sapling density ($b = 0.68$, $p < 0.01$), and land-use duration decreased sapling richness ($b = -0.28$, $p = 0.02$), whereas more mechanical tillage type decreased sapling evenness ($b = -0.11$, $p = 0.04$) (Table 2). The relationships between soil type, topography, soil properties, land-use practices and vegetation together were evaluated with a path model. We found that on steep slopes tractors were used less frequently (Figure 4).

In Loma Bonita, soil properties had generally no significant effect on vegetation cover or sapling diversity. Only soil pH was

TABLE 1 The relationships between the history of land-use practices and soil properties for Nizanda and Loma Bonita.

		Extent and duration		Intensity				Frequency	
		Total duration	Field size	Stocking density	Tractor use	Tillage type	Fertilizer use	Herb/pest frequency	Weeding frequency
Nizanda	OM					−0.81*			
	pH		−0.31						
	N					−0.07		0.04	
	P		−0.49*			−0.93*			
	EC						0.02*	0.02*	
	Mg	−0.36*	−0.45*						1.00*
	Ca			−0.62		−0.63			
	K				−0.15	−0.05		0.04	
	Fe	−0.49*				−0.60*			
	Cu	−0.64*			1.70*		−0.53*	0.64*	
	Zn						1.22		
	Mn				1.37*				

		Extent and duration		Intensity			Frequency	
		Total duration	Months land use/yr	Stocking density	Trees planted	Exotic grass planted	Herb/pest frequency	Fire events
Loma Bonita	BD		−0.07	0.08		−0.22*		
	OM							
	pH		−0.28	−0.30				
	N			−0.04				
	EC			−0.02				
	Ca			−0.52*				
	Na	0.03						0.03
	Fe			0.48				
	Cu	0.40	−0.42*	−0.70*	0.73			0.43
	Zn			−0.66*		0.86	−0.49	
	Mn		0.37*					0.66*

Note: Numbers in the table are the averaged and standardized regression coefficients of the linear models, based on the best models with Akaike information criterion (AICc) <2. All relationships shown are significant ($p<0.05$) with highly significant relationships ($p<0.01$) indicated with an asterisk.

associated with increased bare soil cover ($b=0.48$, $p=0.04$) and sapling density ($b=0.43$, $p=0.04$) (Table 2). Previous land-use practices did significantly affect grass, palm and climber cover, and sapling density and evenness. Land-use duration increased palm cover ($b=0.15$, $p=0.02$) and decreased cover of herbaceous climbers ($b=-0.80$, $p=0.04$). The planting of exotic grasses increased grass cover ($b=1.5$, $p=0.03$) and sapling density ($b=1.11$, $p=0.02$). The number of fire events decreased the cover of herbaceous climbers ($b=-0.94$, $p<0.01$), and weeding frequency increased grass cover ($b=0.65$, $p=0.02$) but decreased sapling evenness ($b=-0.09$, $p=0.04$) (Table 2). When analysing the relationships between soil type, topography, soil properties, land-use practices and vegetation together through path analysis, we found that on steep slopes there is a higher weeding frequency, leading to a higher grass cover, which in turn decreases tree cover (Figure 4).

4 | DISCUSSION

In this study we analysed how soil type, topography, land-use history and soil properties affect early succession in abandoned agricultural fields in two rural Mexican communities (Figure 1). Land-use practices were clearly associated with the characteristics of the landowner (residence time, rural or urban origin), whereas soil type and topography mainly constrained or facilitated land-use practices. For Nizanda, soil nutrients were mainly related to a more mechanical tillage type (e.g. decrease N, K) and a higher frequency of use of herbicides and pesticides use (e.g. increase N, K), whereas for Loma Bonita a higher stocking density had the largest effect on a range of soil properties (e.g. increase bulk density, decrease pH, N) (Table 1). We found that where high-intensive land management was implemented, such as tractor use in Nizanda, it is the use of this management measure that affects early succession

TABLE 2 Relationships between the history of land-use practices and soil properties, and the grass, tree and sapling attributes.

		Extent and duration		Intensity		Soil
		Total duration	Field size	Tractor use	Tillage type	*K*
Nizanda	Tree cover (%)			−1		
	Sapling density		**0.68***			
	Sapling richness	−0.28		**−1***		0.40
	Sapling evenness				−0.11	

		Duration	Intensity		Frequency			Soil
		Months land use/yr	Stocking rate	Exotic grass planted	Herb/pest frequency	Weeding frequency	Fire events	pH
Loma Bonita	Grass cover (%)	0.43			0.57	**0.80***	0.53	
	Sapling density		**0.66***	1				0.43
	Sapling evenness					−0.09		

Note: Results for both Nizanda and Loma Bonita are depicted. Numbers in the table are the averaged and standardized regression coefficients of the linear models, based on the best models with Akaike information criterion (AICc) <2. All relationships shown are significant ($p<0.05$) with highly significant relationships ($p<0.01$) indicated with an asterisk.

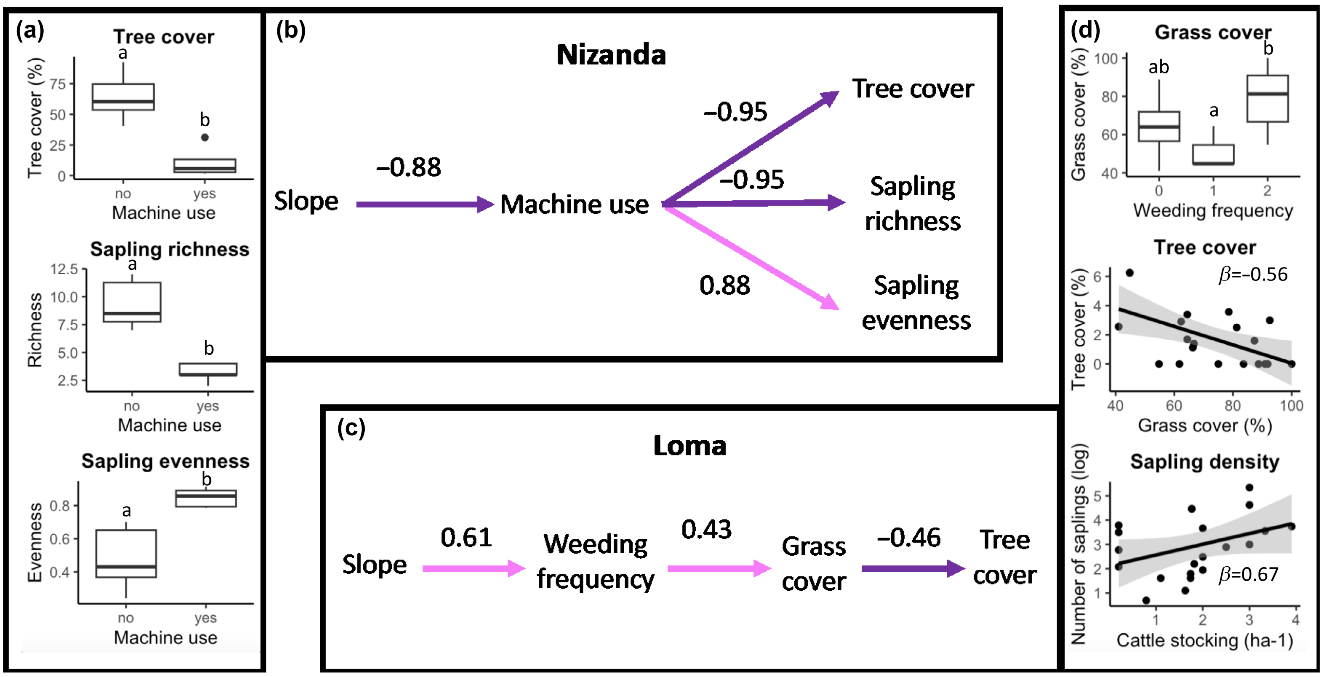

FIGURE 4 The effect of slope and land management practices on vegetation and sapling abundance and diversity in Nizanda (a, b) and Loma Bonita (c, d). The results of the path models for Nizanda (b, $n=14$) and Loma Bonita (c, $n=19$) are visualized in the centre of the graph. The models are composed based on the results of the linear models, and these two models display the best-fit models. The path coefficients are visualized, and the colour of the arrow corresponds to the direction of the coefficient, either positive (pink) or negative (purple). All relationships depicted here are significant ($p<0.05$), except for the relationship between weeding frequency and grass cover ($p=0.06$). In the right- and left-hand panels, the significant relationships between land-use practices and vegetation are visualized as boxplots or as linear relationship.

most (Figure 4). By contrast, in Loma Bonita, where no machinery is used, it is the frequency of the land-use practices, in this case weeding frequency, which mainly affects tree cover and establishment. In the following, the results are discussed in more detail, followed by management implications.

4.1 | Landowners and land-use practices

Nizanda and Loma Bonita differ in many ecological aspects, such as climate, and in social aspects, such as time of establishment, history, local language, cultural background and land-use practices

(Berget et al., 2021). As a result, they represent two distinctly different socio-ecological systems, leading to contrasting successional pathways (Balvanera et al., 2021). In Nizanda, seedling establishment was mainly inhibited through the previous use of machinery, whereas in Loma Bonita mainly the competition with grasses slowed down seedling establishment and might potentially arrest succession (Figure 4). In both communities the previous residence of the landowner (rural or urban) and the time of residence in the current community affected the land-use practices (Figure 3). People who lived in an urban setting before moving to Nizanda had more cattle, which might be explained by the possession of more financial resources to move beyond the traditional maize cultivation and buy more cows (Li Ng & Serrano, 2017). The longer people lived in Nizanda, the more fertilizer they used, which might be a consequence of soil nutrient depletion as the land has been used for a longer period (Certini, 2005; Styger et al., 2007; Runyan et al., 2012).

In Loma Bonita, longer-term residents tend to come from urban areas, because this is a relatively young community, and the first settlers established Loma Bonita in the 1970s, whereas younger residents have been born in this new community (Berget et al., 2021). Long-term residents also own larger fields on more fertile eutric cambisols, which change less frequently from owner to owner, and have a higher cattle grazing intensity. These results together might indicate that the earlier residents had the opportunity to choose larger and better fields with a higher agricultural value (Figure 3). They also use fewer herbicides, which may be because of a lower need to optimize production because of the larger area they own on the more fertile soil.

Therefore, at both sites the previous residence and residence time of the landowner are important factors that affect land-use practices. This indicates that personal experiences, and cultural, human and financial capital and support shape people's opportunities and management decisions (Berget et al., 2021). It is unclear whether young, local villagers have different practices because they have less power and access to resources, or because they have a different interest and are open to a different way of farming. Therefore, we recommend for future research the evaluation of external factors and the policy landscape on the farmers' decision on land-use practices, including the market demand, governmental subsidies, and inequality and poverty constraining the farmers' choices and possibilities.

4.2 | Soil and land use

Soil type and topography determine the biophysical potential for different types of land use, and therefore shape the land-use practices in both communities (Heinze et al., 2020). In Nizanda, fluvisols and regosols are common on flat terrain, which allows for mechanical tillage using a tractor. In particular, fluvisols were expected to have a higher EC because these soils are generally fertile, but mechanical tillage can reduce the amount of organic matter through reduced plant residue input and increased carbon oxidation and, hence, reduce the EC of the soil (Ramos et al., 2018; ISRIC World Soil Information, 2023; Jakab et al., 2023). We found that mechanical tillage indeed decreased soil N and K, but did not significantly affect EC (Table 1). On soils with a higher clay content there is a more frequent use of herbicide/pesticide and higher weeding frequency, suggesting that plants, including weeds, grow better on clayey soils. Because we did not find a significant relationship between soil clay percentage and soil nutrients, it might be the water-holding capacity of the soil that enhances plant growth in this dry forest system (Gaiser et al., 2000). We expected and found that more fertile soils (i.e. higher soil N, K and EC) had a higher herbicide/pesticide use frequency, probably because fertile soils are more productive and therefore need more weed control.

In Loma Bonita, dystric cambisols are less intensively used for cattle grazing, probably the grass *Kyllinga brevifolia* (Rottb.) Hassk. occurs on these soils. Farmers consider this species to be a weed because it is not edible for cows. Farmers control *Kyllinga brevifolia* using fire, which explains the higher fire frequency on dystric cambisols. Interestingly, the stocking density of cattle had the strongest effect on soil properties (Table 1). Stocking density increased soil bulk density, probably because of trampling, whereas it decreased soil nutrients (N, EC) and pH, probably because grazing leads to nutrient removal by cows (Asner et al., 2004; Geissen et al., 2009). In sum, soil types and topography affect land-use practices, whereas, in turn land-use practices have an effect on soil properties as well. However, the lower statistical power may have resulted in fewer significant results for Nizanda (14 plots in Nizanda, 20 plots in Loma Bonita). A higher plot number with a more equal distribution of plots among the four soil types would increase the statistical power to draw conclusions. The same holds for Loma Bonita, where there are two soil types, but only three plots are located at eutric cambisols.

4.3 | The effects of topography, soil and land-use practices on early succession

For both communities, land-use history left more legacies on the vegetation (22 of the 97 evaluated relationships were significant) than did soils (6 of 36). In Nizanda, tractor use decreased with slope steepness, because heavy machines are not suitable for steeper areas (Figure 4). Tractor use, in turn, decreases tree cover and sapling richness, but increases evenness (Table 2). Tractor use reduced tree cover because stems and stumps are removed before the tractor enters and roots are more thoroughly removed by machines than by manual clearing using a machete (Chinea, 2002). This can also lead to a lower richness of saplings, because it selects for those few species that can survive frequent biomass removal through resprouting or that can tolerate harsh microclimatic conditions by establishing from seed on bare land (Chinea, 2002; Jakovac et al., 2016). Tractor use also increases species evenness, most likely because the ruderal species that thrive under intense management and soil compaction are released from competition by other species, and are therefore present in high numbers.

For Loma Bonita, both planting of fast-growing, nutritious exotic grasses and frequent weeding increase grass cover (Table 2, Figure 4). Weeding favours basal sprouting and hence, the lateral spread of grasses, thus increasing fodder availability for cows (Esquivel et al., 2008). A higher grass cover, in turn, inhibits the establishment of tree seedlings through competition for space, light, water and nutrients (Holl, 1998; Del Castillo & Blanco-Macías, 2007; Peterson & Carson, 2008) and leads therefore to decreased tree cover. This could also be the mechanism that explains why a higher stocking density leads to a higher sapling density, because cows can shorten the grass layer, open up the vegetation or even disperse seeds (Pignataro et al., 2017; Vázquez-Ribera & Martorell, 2022). Frequent weeding also favours woody species able to resprout. The majority of the saplings we observed in the plots are resprouts. Because few woody species are good resprouters, this may explain why frequent weeding reduces tree species evenness (Jakovac et al., 2015). Hence, early successional vegetation is mainly determined by land-use legacies, which are shaped by topography, whereas soil properties play a minor role, according to this study.

4.4 | Management implications

In sum, topography and soil type together affect land use and land management, and the intensity and frequency of these management practices have, in turn, a large effect and clear legacy on early forest recovery on abandoned fields. Therefore, we recommend focusing forest restoration efforts, especially through natural regeneration, on abandoned agricultural lands with a history of low-intensity and low-frequency land-use practices (Guariguata & Ostertag, 2001; Crouzeilles et al., 2016). In these areas, restoration through natural regeneration could reduce restoration costs, enhance natural dynamics, the presence of local tree species and biotic interactions (Chazdon & Guariguata, 2016; Tucker et al., 2023). When restoration is planned in an area with a land-use history including heavy machinery, planting trees to enhance diversity and nucleation are expected to particularly speed up forest recovery (Yarranton & Morrison, 1974; Guevara et al., 1992; de la Peña-Domene et al., 2013; Holl et al., 2020). However, active restoration in an area where exotic grasses are present would benefit from removing the grasses first and planting taller trees that suffer less competition from the grasses (Holl, 1998; Del Castillo & Blanco-Macías, 2007).

Agricultural practices are intensifying with mechanization and the access to chemicals. With a more-efficient food production, less land will be needed to meet demand and lands less suitable for agriculture, based on among other things, topography and soil type, could be used to regrow forests (Latawiec et al., 2015). These secondary forests will not only enhance, for example, the local microclimate and pollination of crops, but can also be financially attractive to local farmers in the form of biodiversity or carbon credits (such as the current governmental program Sembrando Vida in which Loma Bonita is participating). Therefore, regrowing forests on lands with a low-intensity and low-frequency land-use history has ecological and financial benefits.

STATEMENT ON INCLUSION

To our study, authors from a number of different countries contributed, including scientists based in Mexico. Mexican authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

AUTHOR CONTRIBUTIONS

IH, LP, FB, MMR, JM, MvdS and RM conceived the ideas and designed the methodology; IH, RDLM and PJR collected the data; IH and RJ analysed the data; IH led the writing of the manuscript. All authors contributed critically to interpretation of results and the manuscript and gave final approval for publication. The authors do not declare any conflicts of interest.

ACKNOWLEDGEMENTS

We are grateful towards the communities of Nizanda and Loma Bonita, and in particular the Reyes-Manuel family in Nizanda and the Zacarias Vazquez family in Loma Bonita who hosted us, local people who joined the field teams and students from UNAM and WUR who participated in data collection and digitalization.

FUNDING INFORMATION

This research has been funded with an ERC Advanced Grant 'Biodiversity and recovery of forests in tropical landscapes – PANTROP' (ID 834775) granted to Lourens Poorter.

DATA AVAILABILITY STATEMENT

Previous land-use practices and plot vegetation attributes are available in the DANS-EASY database following this link: https://doi.org/10.17026/LS/MUNS0F. The data to simulate the main graphs, and the code used to perform the statistical analyses can be found at GitHub, following this link: https://tinyurl.com/3kwdxybh.

ORCID

Iris Hordijk https://orcid.org/0000-0002-6302-6254
Lourens Poorter https://orcid.org/0000-0003-1391-4875
Miguel Martínez-Ramos https://orcid.org/0000-0002-7785-1917
Frans Bongers https://orcid.org/0000-0002-8431-6189
Masha van der Sande https://orcid.org/0000-0002-6845-2308
Rodrigo Muñoz https://orcid.org/0000-0001-9312-8449
Jorge A. Meave https://orcid.org/0000-0002-6241-8803

REFERENCES

Asner, G.P., Townsend, A.R., Bustamante, M.M.C., Nardoto, G.B. & Olander, L.P. (2004) Pasture degradation in the central Amazon: linking changes in carbon and nutrient cycling with remote sensing. *Global Change Biology*, 10(5), 844–862. Available from: https://doi.org/10.1111/j.1529-8817.2003.00766.x

Balvanera, P., Paz, H., Arreola-Villa, F., Bhaskar, R., Bongers, F., Cortés, S. et al. (2021) MINI REVIEW social ecological dynamics of tropical secondary forests. *Forest Ecology and Management*, 496, 119369. Available from: https://doi.org/10.1016/j.foreco.2021.119369

Berget, C., Verschoor, G., García-Frapolli, E., Mondragón-Vázquez, E. & Bongers, F. (2021) Landscapes on the move: land-use change history in a mexican agroforest frontier. *Landscape*, 10(10), 1066. Available from: https://doi.org/10.3390/land10101066

Bongaarts, J. (2019) IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. *Population and Development Review*, 45(3), 680–681. Available from: https://doi.org/10.1111/padr.12283

Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R. et al. (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, 26(13), 3005–3035. Available from: https://doi.org/10.1007/s10531-017-1453-2

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human–induced species losses: entering the sixth mass extinction. *Science Advances*, 1(5), e1400253. Available from: https://doi.org/10.1126/sciadv.1400253

Celedón Muñiz, H. (2006) *Impacto del sistema agricola de roza, tumba y quema sobre las caracteristicas de tres unidades de suelo en la selva Lacandona de Chiapas*. Mexico City, Mexico: Universidad Nacional Autonoma de Mexico.

Certini, G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia*, 143(1), 88. Available from: https://doi.org/10.1007/s00442-004-1788-8

Chao, A. & Ricotta, C. (2019) Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology*, 100(12), e02852. Available from: https://doi.org/10.1002/ecy.2852

Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1–2), 51–71. Available from: https://doi.org/10.1078/1433-8319-00042

Chazdon, R.L. (2014) Second growth: the promise of tropical Forest regeneration in an age of deforestation-university of Chicago press. *Hyperfine Interactions*, 32(1–4), 111–126.

Chazdon, R.L. & Guariguata, M.R. (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica*, 48(6), 716–730. Available from: https://doi.org/10.1111/btp.12381

Chinea, J.D. (2002) Tropical forest succession on abandoned farms in the Humacao municipality of eastern Puerto Rico. *Forest Ecology and Management*, 167(1–3), 195–207. Available from: https://doi.org/10.1016/S0378-1127(01)00693-4

Clements, F.E. (1916) *Plant succession: an analysis of development in vegetation*. Carnegie Institution of Washington.

Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E.V. & Rey Benayas, J.M. (2016) A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, 7, 11666. Available from: https://doi.org/10.1038/ncomms11666

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A. & Hansen, M.C. (2018) Classifying drivers of global forest loss. *Science (New York, N.Y.)*, 361(6407), 1108–1111. Available from: https://doi.org/10.1126/science.aau3445

de la Peña-Domene, M., Martínez-Garza, C. & Howe, H.F. (2013) Early recruitment dynamics in tropical restoration. *Ecological Applications*, 23(5), 1124–1134. Available from: https://doi.org/10.1890/12-1728.1

Del Castillo, R.F. & Blanco-Macías, A. (2007) Secondary succession under a slash-and-burn regime in a tropical montane cloud forest: soil and vegetation characteristics. In: *Biodiversity loss and conservation in fragmented forest landscapes: the forests of montane Mexico and temperate South America*, pp. 158–180. Wallingford UK: CABI.

Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E. et al. (2016) Resilience of tropical dry forests - a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, 125(10), 1386–1397. Available from: https://doi.org/10.1111/oik.03229

Ellenberg, D. & Mueller-Dombois, D. (1974) Community sampling: the Relevé method. In: *Aims and methods of vegetation ecology*. New York: Wiley and Sons.

Esquivel, M.J., Harvey, C.A., Finegan, B., Casanoves, F. & Skarpe, C. (2008) Effects of pasture management on the natural regeneration of neotropical trees. *Journal of Applied Ecology*, 45(1), 371–380. Available from: https://doi.org/10.1111/j.1365-2664.2007.01411.x

FAO. (2020) *Global Forest resources assessment 2020-key findings*. Rome. FAO.

Fragoso, C.A.R.L.O.S. & Lavelle, P.A.T.R.I.C.K. (1987). The earthworm community of a Mexican tropical rain forest (Chajul, Chiapas). *AM Bonvicini-Pagliai and P. Omodeo*, 281–295.

Gaiser, T., Graef, F. & Cordeiro, J.C. (2000) Water retention characteristics of soils with contrasting clay mineral composition in semi-arid tropical regions. *Australian Journal of Soil Research*, 38(3), 523. Available from: https://doi.org/10.1071/SR99001

Gallardo-Cruz, J.A., Meave, J.A., González, E.J., Lebrija-Trejos, E.E., Romero-Romero, M.A., Pérez-García, E.A. et al. (2012) Predicting tropical dry forest successional attributes from space: is the key hidden in image texture? *PLoS One*, 7(2), e30506. Available from: https://doi.org/10.1371/journal.pone.0030506

Geissen, V., Sánchez-Hernández, R., Kampichler, C., Ramos-Reyes, R., Sepulveda-Lozada, A., Ochoa-Goana, S. et al. (2009) Effects of land-use change on some properties of tropical soils - an example from Southeast Mexico. *Geoderma*, 151(3–4), 87–97. Available from: https://doi.org/10.1016/j.geoderma.2009.03.011

Griscom, H.P., Griscom, B.W. & Ashton, M.S. (2009) Forest regeneration from pasture in the dry tropics of Panama: effects of cattle, exotic grass, and forested riparia. *Restoration Ecology*, 17(1), 117–126. Available from: https://doi.org/10.1111/j.1526-100X.2007.00342.x

Guadarrama-Chávez, P., Camargo-Ricalde, S.L., Hernández-Cuevas, L. & Castillo-Argüero, S. (2007). Los hongos micorrizógenos arbusculares de la región de Nizanda, Oaxaca, México. *Botanical Sciences*, 81, 131–137.

Guariguata, M.R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, 148(1–3), 185–206. Available from: https://doi.org/10.1016/S0378-1127(00)00535-1

Guevara, S., Meave, J., Moreno-Casasola, P. & Laborde, J. (1992) Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science*, 3(5), 655–664. Available from: https://doi.org/10.2307/3235833

Heinimann, A., Mertz, O., Frolking, S., Christensen, A.E., Hurni, K., Sedano, F. et al. (2017) A global view of shifting cultivation: recent, current, and future extent. *PLoS One*, 12(9), e0184479. Available from: https://doi.org/10.1371/journal.pone.0184479

Heinze, A., Bongers, F., Ramírez Marcial, N., García Barrios, L. & Kuyper, T.W. (2020) The montane multifunctional landscape: how stakeholders in a biosphere reserve derive benefits and address trade-offs in ecosystem service supply. *Ecosystem Services*, 44, 101134. Available from: https://doi.org/10.1016/j.ecoser.2020.101134

Hoang, N.T. & Kanemoto, K. (2021) Mapping the deforestation footprint of nations reveals growing threat to tropical forests. *Nature Ecology & Evolution*, 5(6), 845–853. Available from: https://doi.org/10.1038/s41559-021-01417-z

Holl, K.D. (1998) Effects of above- and below-ground competition of shrubs and grass on Calophyllum brasiliense (Camb.) seedling growth in abandoned tropical pasture. *Forest Ecology and Management*, 109(1–3), 187–195. Available from: https://doi.org/10.1016/S0378-1127(98)00248-5

Holl, K.D., Reid, J.L., Cole, R.J., Oviedo-Brenes, F., Rosales, J.A. & Zahawi, R.A. (2020) Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. *Journal of Applied Ecology*, 57(12), 2316–2328. Available from: https://doi.org/10.1111/1365-2664.13684

Hordijk, I., Meijer, F., Nissen, E., Boorsma, T. & Poorter, L. (2019) Cattle affect regeneration of the palm species Attalea princeps in a Bolivian forest–savanna mosaic. *Biotropica*, 51(1), 28–38. Available from: https://doi.org/10.1111/btp.12613

Hordijk, I., Poorter, L., Martinez-Ramos, M., Bongers, F., Muñoz, R. & Meave, J.A. (2023) Efectos de la historia de uso del suelo y de la cobertura forestal en el paisaje sobre la recuperación de bosques. *Boletín de la Sociedad Científica Mexicana de Ecología*, 3(9), 34–41.

Iskandar, J., Iskandar, B.S. & Partasasmita, R. (2018) Site selection and soil fertility management by the outer baduy people (Banten, Indonesia) in maintaining swidden cultivation productivity. *Biodiversitas*, 19(4), 1334–1346. Available from: https://doi.org/10.13057/biodiv/d190421

ISRIC. (2023) *World soil information*. Wageningen: ISRIC.

IUSS Working Group WRB. (2012) *World reference base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps*. 4th edition. Vienna, Austria: Internation Union of Soil Sciences (IUSS).

Jakab, G., Madarász, B., Masoudi, M., Karlik, M., Király, C., Zacháry, D. et al. (2023) Soil organic matter gain by reduced tillage intensity: storage, pools, and chemical composition. *Soil and Tillage Research*, 226, 105584. Available from: https://doi.org/10.1016/j.still.2022.105584

Jakovac, C.C., Bongers, F., Kuyper, T.W., Mesquita, R.C.G. & Peña-Claros, M. (2016) Land use as a filter for species composition in Amazonian secondary forests. *Journal of Vegetation Science*, 27(6), 1104–1116. Available from: https://doi.org/10.1111/jvs.12457

Jakovac, C.C., Junqueira, A.B., Crouzeilles, R., Peña-Claros, M., Mesquita, R.C.G. & Bongers, F. (2021) The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biological Reviews*, 96(4), 1114–1134. Available from: https://doi.org/10.1111/brv.12694

Jakovac, C.C., Peña-Claros, M., Kuyper, T.W. & Bongers, F. (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology*, 103(1), 67–77. Available from: https://doi.org/10.1111/1365-2745.12298

Kim, J.H. (2019) Multicollinearity and misleading statistical results. *Korean Journal of Anesthesiology*, 72(6), 558–569.

Latawiec, A.E., Strassburg, B.B.N., Brancalion, P.H.S., Rodrigues, R.R. & Gardner, T. (2015) Creating space for large-scale restoration in tropical agricultural landscapes. *Frontiers in Ecology and the Environment*, 13(4), 211–218. Available from: https://doi.org/10.1890/140052

Lebrija-Trejos, E., Bongers, F., Pérez-García, E.A. & Meave, J.A. (2008). Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*, 40(4), 422–431.

Li Ng, J.J. & Serrano, C. (2017) *Income in Mexico and Evolution of Poverty: Notes on the New ENIGH 2016*.

Lohbeck, M., Albers, P., Boels, L.E., Bongers, F., Morel, S., Sinclair, F. et al. (2020) Drivers of farmer-managed natural regeneration in the Sahel: Lessons for Restoration. *Scientific Reports*, 10(1), 70746. Available from: https://doi.org/10.1038/s41598-020-70746-z

Martínez, L.J. & Zinck, J.A. (2004) Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia. *Soil and Tillage Research*, 75(1), 3–18. Available from: https://doi.org/10.1016/j.still.2002.12.001

Martínez-Ramos, M., Pingarroni, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeño-Hernández, I. & Bongers, F. (2016) Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica*, 48(6), 12382. Available from: https://doi.org/10.1111/btp.12382

Mazerolle, M.J. (2023). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.3, https://cran.r-project.org/package=AICcmodavg.

Meyfroidt, P. (2013) Environmental cognitions, land change, and social-ecological feedbacks: an overview. *Journal of Land Use Science*, 8(3), 341–367. Available from: https://doi.org/10.1080/1747423X.2012.667452

Muñoz, R., Enríquez, M., Bongers, F., López-Mendoza, R.D., Miguel-Talonia, C. & Meave, J.A. (2023) Lithological substrates influence tropical dry forest structure, diversity, and composition, but not its dynamics. *Frontiers in Forests and Global Change*, 6, 1082207. Available from: https://doi.org/10.3389/ffgc.2023.1082207

Nanni, A.S., Sloan, S., Aide, T.M., Graesser, J., Edwards, D. & Grau, H.R. (2019) The neotropical reforestation hotspots: a biophysical and socioeconomic typology of contemporary forest expansion. *Global Environmental Change*, 54, 148–159. Available from: https://doi.org/10.1016/j.gloenvcha.2018.12.001

Pérez-García, E.A., Meave, J.A., Villaseñor, J.L., Gallardo-Cruz, J.A. & Lebrija-Trejos, E.E. (2010) Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico. *Folia Geobotanica*, 45(2), 143–161. Available from: https://doi.org/10.1007/s12224-010-9064-7

Peterson, C.J. & Carson, W.P. (2008) Tropical forest community ecology. In: Carson, W.P. & Schnitzer, S.A. (Eds.) *Experimental agriculture*, Vol. 45. Chichester, UK: Wiley-Blackwell, p. 382.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987) A hierarchical consideration of causes and mechanisms of succession. *Vegetatio*, 69(1–3), 109–114. Available from: https://doi.org/10.1007/BF00038691

Pignataro, A.G., Levy-Tacher, S.I., Aguirre-Rivera, J.R., Nahed-Toral, J., González-Espinosa, M., González-Arzac, A. et al. (2017) Natural regeneration of tree species in pastures on peasant land in Chiapas, Mexico. *Agriculture, Ecosystems and Environment*, 249, 137–143. Available from: https://doi.org/10.1016/j.agee.2017.08.020

Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F. et al. (2021) Multidimensional tropical forest recovery. *Science*, 374(6573), 1370–1376. Available from: https://doi.org/10.1126/science.abh3629

Poorter, L., van der Sande, M.T., Amissah, L., Bongers, F., Hordijk, I., Kok, J. et al. (2024) A comprehensive framework for vegetation succession. *Ecosphere*, 15(4), e4794. Available from: https://doi.org/10.1002/ecs2.4794

Ramos, F.T., de Dores, E.F.C., do Weber, O.L.S., Beber, D.C., Campelo, J.H. & Maia, J.C.D.S. (2018) Soil organic matter doubles the cation exchange capacity of tropical soil under no-till farming in Brazil. *Journal of the Science of Food and Agriculture*, 98(9), 3595–3602. Available from: https://doi.org/10.1002/jsfa.8881

Rauzi, F. & Hanson, C.L. (1966) Water intake and runoff as affected by intensity of grazing. *Journal of Range Management*, 19(6), 351. Available from: https://doi.org/10.2307/3895570

Reina, L. (1991) Los albores de la modernidad: El ferrocarril de Tehuantepec. *'Anuario VIII'. (Instituto de Investigaciones Humanísticas, Universidad Veracruzana: Xalapa, Ver., Mexico)*, 10–22.

Runyan, C.W., D'Odorico, P. & Lawrence, D. (2012) Effect of repeated deforestation on vegetation dynamics for phosphorus-limited tropical forests. *Journal of Geophysical Research: Biogeosciences*, 117(1), 1841. Available from: https://doi.org/10.1029/2011JG001841

Rzedowski, J. & Huerta, L. (1978). *Vegetación de México* (Vol. 432). México: Editorial Limusa.

Sanchez, G. (2013) *PLS path modeling with R*. R Package Notes. Berkeley: Trowchez Editions, 383, 551. http://www.gastonsanchez.com/PLSPathModelingwithR.pdf

Seo, S.N. & Mendelsohn, R. (2008) An analysis of crop choice: adapting to climate change in south American farms. *Ecological Economics*, 67(1), 109–116. Available from: https://doi.org/10.1016/j.ecolecon.2007.12.007

Siebe, C., Martínez-Ramos, M., Segura-Warnholtz, G., Rodríguez-Velázquez, J. & Sánchez-Beltrán, S. (1996) Soil and vegetation patterns in the tropical rainforest at Chajul, southeast Mexico. In: Simmorangkir, D. (Ed.) *Proceedings of the international congress on soils of tropical Forest ecosystems*, Balikpapan, Indonesia, Vol. 8, pp. 40–58.

Styger, E., Rakotondramasy, H.M., Pfeffer, M.J., Fernandes, E.C.M. & Bates, D.M. (2007) Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture, Ecosystems and Environment*, 119(3–4), 257–269. Available from: https://doi.org/10.1016/j.agee.2006.07.012

Tucker, N.I., Elliott, S., Holl, K.D. & Zahawi, R.A. (2023) Restoring tropical forests: lessons learned from case studies on three continents. In: *Ecological restoration: moving forward using lessons learned*. Cham: Springer International Publishing, pp. 63–101.

Van Der Sande, M.T., Powers, J.S., Kuyper, T.W., Norden, N., Salgado-Negret, B., Silva De Almeida, J. et al. (2023) Soil resistance and recovery during neotropical forest succession. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 378(1867). Available from: https://doi.org/10.1098/rstb.2021.0074

Vázquez-Ribera, C. & Martorell, C. (2022) The effects of livestock grazing on vegetation in a semiarid grassland: a test of three hypotheses. *Applied Vegetation Science*, 25(2), e12656. Available from: https://doi.org/10.1111/avsc.12656

Villa, P.M., Martins, S.V., de Oliveira Neto, S.N., Rodrigues, A.C., Martorano, L.G., Monsanto, L.D. et al. (2018) Intensification of shifting cultivation reduces forest resilience in the northern Amazon. *Forest Ecology and Management*, 430, 312–320. Available from: https://doi.org/10.1016/j.foreco.2018.08.014

Yarranton, G.A. & Morrison, R.G. (1974) Spatial dynamics of a primary succession: nucleation. *The Journal of Ecology*, 62(2), 417. Available from: https://doi.org/10.2307/2258988

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J. & Martínez-Ramos, M. (2015) Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, 18(3), 443–455. Available from: https://doi.org/10.1111/avsc.12161

Zermeño-Hernández, I., Pingarroni, A. & Martínez-Ramos, M. (2016) Agricultural land-use diversity and forest regeneration potential in human- modified tropical landscapes. *Agriculture, Ecosystems and Environment*, 230, 210–220. Available from: https://doi.org/10.1016/j.agee.2016.06.007

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Figures.

Figure S1. Diagram depicting the of vegetation measurements performed in a plot.

Figure S2. Cluster analysis of land use variables of plots in Nizanda.

Figure S3. Cluster analysis of land use variables of the plots in Loma Bonita.

Appendix S2. Tables.

Table S1. Interview questions.

Table S2. Overview of the growth form categories in which the plants were categorised.

Table S3. Overview variables.

Table S4. Coefficients table linear models soil properties and vegetation attributes.

Table S5. Coefficients table linear models soil properties, land use practices and vegetation attributes.

How to cite this article: Hordijk, I., Poorter, L., Martínez-Ramos, M., Bongers, F., Mendoza, R.D.L., Romero, P.J. et al. (2024) Land use legacies affect early tropical forest succession in Mexico. *Applied Vegetation Science*, 27, e12784. Available from: https://doi.org/10.1111/avsc.12784