



Vegetation structure and biodiversity recovery in 19-year-old active restoration plantations in a Neotropical cloud forest

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Abstract

Aim of study: To evaluate how middle-aged active restoration plantations of native tree species contribute to the recovery of the tropical cloud forest in terms of vegetation structure, tree richness, species composition, and to shade-tolerance and seed dispersal mode functional groups.

Area of study: We studied two 19-year-old active restoration sites and their reference mature forests in the tropical montane cloud forest belt, Veracruz, Mexico.

Materials and methods: The basal area, density and height as well as the tree species composition and number of species and individuals classified by shade tolerance (pioneer and non-pioneer trees), and seed dispersal mode (anemochorous, barochorous-synzoochorous and endozoochorous) were compared between active restoration plantations and reference forests.

Main results: Planted trees and the woody vegetation growing under them represented a high proportion of reference forests' basal area. Tree richness and Shannon's equitability index were similar in both reference forests and one active restoration plantation and slightly different in the other. Tree species composition differed among sites; however, each 19-year-old plantation already had several non-pioneer species and a similar species proportion of the seed dispersal syndromes present in their reference forests.

Research highlights: Active restoration accelerated the recovery of cloud forest in degraded pasture and bracken fern lands. Planted trees promoted the rapid development of vegetation structure and natural tree regeneration. Although species composition is still different, these middle-aged restoration plantations already have forest species and a proportion of functional groups of species similar to those of their own reference montane cloud forests.

Keywords: active restoration; forest recovery; passive restoration; seed dispersal mode; succession; tree species; tropical montane cloud forest.

Authors' contributions: Conceived and designed the study: RAP and GWL. Analyzed data and wrote the paper: GWL. Acquired data, discussed results, and agreed with final version of the manuscript: RAP, GWL, TNS.

Citation: Pedraza, R.A., Williams-Linera, G., Nicolás-Silva, T. (2021). Vegetation structure and biodiversity recovery in 19-year-old active restoration plantations in a Neotropical cloud forest. *Forest Systems*, Volume 30, Issue 1, e004. <https://doi.org/10.5424/fs/2021301-17131>.

Supplementary material: Tables S1 and S2 accompany the paper on FS website.

Received: 03 Jul 2020. **Accepted:** 12 Mar 2021.

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Funding: The study was funded by CONACYT (Mexican Council of Science and Technology).

Competing interests: The authors have declared that no competing interests exist.

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Introduction

Tropical montane cloud forest (TMCF) has been recognized as a highly biodiverse provider of ecosystem services such as a steady supply of high-quality water and protection against soil erosion, however, it is clearly one of the most threatened terrestrial ecosystems (Scatena *et al.*, 2010). Ecological restoration has become crucial for the conservation of biodiversity and ecosystem services, but forest restoration can take decades. Existing reports are mainly based on relatively recently established plantations and rarely include old plantations (*e.g.*, Wortley *et*

al., 2013; Gatica-Saavedra *et al.*, 2017). Forest restoration has been widely implemented in the Neotropics, and several studies have carried out empirical assessments focused most frequently on short-term restoration sites (1 to 15 years old). There have been a few studies on restoration sites of an intermediate age (> 12 – 20 years), and projects on sites over 35 years old are uncommon (*e.g.*, Wortley *et al.*, 2013; Suganuma *et al.*, 2014; Gatica-Saavedra *et al.*, 2017). The recovery of an ecosystem takes time; however, little is known about the long-term performance of old planted trees, or about the recovery of vegetation structure, richness and composition. It is important to measure

the success of forest restoration in the later stages of the process, 10 or more years after starting restoration efforts, because short-term observations may not be reliable predictors of long-term ecosystem responses or successional trajectories (Gatica-Saavedra *et al.*, 2017).

An increasing number of ecological restoration projects are reaching mature ages, thus medium- and even long-term data from ecological restoration experiences are becoming available, and this allows us to assess recovery using ecological indicators and evaluate their success (Holl & Aide, 2010; Sugiama & Durigan, 2015). The majority of empirical evaluations of ecological restoration have focused mainly on the recovery of forest structure as the most rapid and efficient means of assessing a site's condition, with richness, diversity, or species composition used as an indicator of successional stage, and the seed dispersal syndromes operating in the site as indicators of ecological processes (Ruiz-Jaen & Aide 2005a, b; Wortley *et al.*, 2013; Sugiama & Durigan, 2015).

Neotropical forest restoration projects of an intermediate age and older report that after ca. 20-50 years, restoration sites increasingly resemble a mature forest in basal area, canopy cover, height, tree species richness, and tree species composition (*e.g.*, Garcia *et al.*, 2016; Wilson & Rhemtulla, 2016; Trujillo-Miranda *et al.*, 2018), but that 60-100 years is necessary to reestablish species composition (Bechara *et al.*, 2016). Throughout the recovery of vegetation structure, richness and tree species composition, the functional recovery of the system has been monitored using indicators such as the proportion of pioneer to non-pioneer forest species and seed dispersal syndrome. Restoration plantations favor an increase in structure over time as well as changes in the proportion of tree species guilds across trajectories of forest recovery. The turnover of pioneer to forest species has been documented in chronosequences and comparisons of young and old plantations, and natural regeneration (Muñiz-Castro *et al.*, 2006, 2012; Sugiama & Durigan 2015). There is extensive documentation for species dispersed by animals, wind and autochory indicating that plants in forests undergoing restoration and planted forests have a much greater proportion of animal-dispersed trees undergoing natural regeneration than unplanted sites characterized by wind-dispersed species do (*e.g.*, Aubin *et al.*, 2008; Sugiama *et al.*, 2014; Reid *et al.*, 2015; Wilson & Rhemtulla, 2016). In a chronosequence of TMCF in Mexico, the proportion of species and individuals of wind-dispersed tree declined and that of endozoochorous trees remained constant, while that of barochorous-synzoochorous trees increased (Muñiz-Castro *et al.*, 2012).

This study is part of a long-term line of research on ecological restoration of TMCF in central Veracruz, Mexico. In this particular study, we evaluated our restoration project after 19 years. Restoration plantations were used to monitor vegetation structure, richness, diversity, and tree

species composition and the sets of species representing functional guilds. The objective was to determine the degree of recovery of vegetation structure and tree species biodiversity in these middle-aged restoration plantations, with the specific objectives of comparing patterns of vegetation structure, tree richness, diversity and species composition between middle-aged plantations and nearby cloud forest fragments. Also, as an indicator of functional recovery, we explored patterns of biodiversity recovery using all species together and classified as pioneer and non-pioneer species and by seed dispersal mode. Our main hypothesis is that active restoration will accelerate successional recovery of basal area, density, and richness relative to reference forests. Also, we hypothesize that the proportion of functional indicator groups will be recovered in the plantations based on the reference forests.

Materials and Methods

Study area

This study was carried out in the tropical montane cloud forest region of central Veracruz, Mexico. The climate is mild and humid year-round. Total annual precipitation is ca. 1600 mm and mean temperature is 14-18 °C. In this area, we selected two locations. Xolostla (XO, 19° 32' 13"N, 96° 58' 06"W, 1430 m a.s.l.), which was converted to pasture in 1980, and abandoned after 10 years of use, at which time it had a few *Acacia pennatula* (Schltdl. & Cham.) Benth. trees. Mesa Yerba (MY, 19°33' 42" N, 97° 01' 21" W, 1875 m a.s.l.) was deforested for wood and carbon extraction, and abandoned in 1990 at which time it was dominated by *Pteridium arachnoideum* (Kaulf.) Maxon. A detailed disturbance history for each location is given in Pedraza & Williams-Linera (2003).

In 1998, ecological restoration plantations were established at each site. In six 30 × 36 m blocks, 720 seedlings of four native tree species were planted, 10 seedlings of each species along three lines with 3 m spacing between lines. The species used were *Carpinus tropicalis* Walt., *Juglans pyriformis* Liebm., *Liquidambar styraciflua* L. and *Podocarpus matudae* Lundell. The vegetation around each tree planted was cleared with a machete during the first 18 months, then once in 2004 and again in 2014 (Pedraza & Williams-Linera, 2003; Williams-Linera *et al.*, 2016).

Experimental design

In 2016-2017, we monitored the trees planted in both plantations. Each tagged tree was located or declared a non-survivor. All planted trees were surveyed, their diameter was measured at 1.3 m above ground level, and height was

estimated using a clinometer. We selected a forest fragment near each plantation (< 1 km away) as its reference forest. Our original databases consisted of ten 10 m x 10 m plots in each reference forest and were used to analyze tree species composition and vegetation structure. In each plantation, ten 10 m x 10 m plots were distributed throughout the planted area randomly. In each plot, tree species ≥ 5 cm diameter were measured, counted and identified. Unknown species were collected for later identification in the XAL herbarium of the Institute of Ecology, A.C. (INECOL). Scientific names were checked using the Tropicos database (www.tropicos.org) of the Missouri Botanical Garden. Richness (S), the Shannon diversity index (H') and the Shannon equitability index ($E_H = H'/\ln S$) were estimated per site.

The successional stages used to classify tree species were pioneer (shade-intolerant) and non-pioneer or forest tree species based on previously published research, unpublished shade-tolerance databases and field observations (Muñiz-Castro *et al.*, 2006; López-Gómez *et al.*, 2008). For the tree species, seed dispersal mode follows van der Pijl (1972): anemochorous (seeds dispersed by wind), barochorous-synzoochorous (large seeds dispersed by gravity or animals that do not ingest the seeds) and endozoochorous (small seeds dispersed by birds and small mammals) (Muñiz-Castro *et al.*, 2006; López-Gómez *et al.*, 2008).

Statistical analyses

Basal area, density and mean and maximum height were calculated for all plots, and differences between active restoration (planted trees and woody plant regeneration) and reference forests were tested with Student's t-test, using a significance level of $p < 0.05$. Prior to running the t-test, data normality (Shapiro-Wilk's test, $p > 0.05$) was assessed and the data log-transformed when necessary (basal area, mean and maximum height). Statistical analyses were run in JMP v. 10.0.0 (SAS Institute, Cary, NC, USA). Values reported are mean \pm SE unless otherwise indicated.

The number of species and individuals classified by shade tolerance and seed dispersal mode were compared between active plantations (natural regeneration only) and reference forests using the G statistic for the log-likelihood ratio goodness-of-fit test (G-test). To describe similarities in both the species composition and abundance of tree species in the active restoration (without planted trees) and forests, we used nonmetric multidimensional scaling (NMDS). The presence of groups of sites was determined using a matrix of 40 plots and 36 species with two or more individuals. This analysis was carried out in autopilot mode, slow and thorough, Sørensen distance measurements, and 500 iterations. Ordination was run in PC-ORD software (McCune & Grace, 2002).

Results

Planted tree species performed differently between the two 19-year-old active restoration plantations; *Liquidambar styraciflua* had a higher basal area and better survival in MY than in XO, whereas *Juglans pyriformis* and *Podocarpus matudae* grew and survived better in XO than in MY, and *Carpinus tropicalis* had relatively high values of both variables in MY and XO (Table S1 [suppl.]). Survival in planted trees was 59% and 44% in XO and MY, respectively. The basal area of planted trees was 7.2 and 7.9 m²/ha, while density was 658 and 493 trees/ha in XO and MY, respectively. Planted tree species reached a maximum average height of 5 to 16 m (Table S1 [suppl.]).

Overall, the vegetation structure values for the active restoration (including both planted trees and natural regeneration) were close to those of the reference forests (Fig. 1). In XO, the forest had a higher basal area than active restoration ($t = 4.10$, $p = 0.0007$, Fig. 1a). In MY, basal area did not differ between forest and active restoration

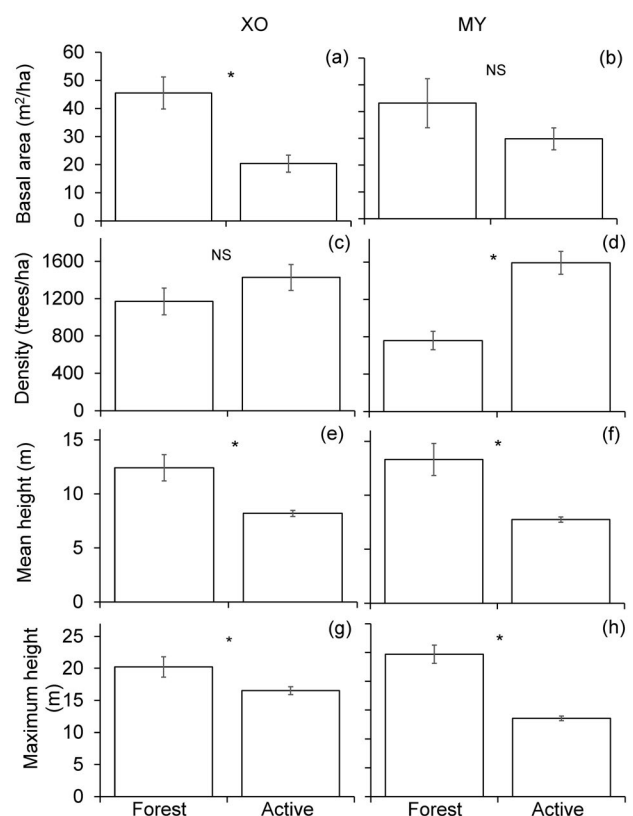


Figure 1. Vegetation structure in the Xolostla (XO) and Mesa Yerba (MY) cloud forest areas of central Veracruz, Mexico. Sites are mature forest and 19-year-old active restoration (planted trees and natural regeneration). Basal area (a, b), density (c, d), mean height (e, f), maximum mean height (g, h). Values are the mean and standard error are shown. * indicates significant differences between means ($p < 0.05$) and NS indicates non-significant differences.

($t = 0.60$, $p = 0.56$; Fig. 1b). Tree density in XO did not differ between sites ($t = 1.29$, $p = 0.21$; Fig. 1c), but in the MY tree density was higher in active restoration than in the forest ($t = 5.29$, $p < 0.0001$; Fig. 1d). Forests had a higher mean (XO, $t = 4.16$, $p = 0.0017$; MY, $t = 4.95$, $p = 0.0004$; Fig. 1e, f) and maximum height (XO, $t = 2.32$, $p = 0.039$; MY, $t = 7.88$, $p < 0.0001$; Fig. 1h, g) than the restoration plantations.

In total, 49 tree species > 5 cm diameter were recorded (Table S2 [suppl.]). In the reference forests, richness was 14 tree species in XO and 21 in MY. In plantations, woody regeneration included 16 tree species in XO and 15 in MY (Table S2 [suppl.]). Shannon's equitability index tended to be similar in both XO and MY reference forests (0.85 and 0.83, respectively), and also in XO active restoration (0.86), but was lower in MY active restoration (0.75) (Table S2 [suppl.]).

The proportion of tree species classified as pioneer and non-pioneer was different in forest and active restoration in XO and was similar in MY (G-test = 6.02, $p < 0.05$, G-test = 1.78, $p > 0.05$, respectively, Fig. 2a). However, the proportion of individuals differed between treatments (XO G-test = 75.91, MY G-test = 68.6, $p < 0.01$, Fig. 2b). Non-pioneers represented $> 75\%$ of the tree species, and $> 90\%$ of the individuals in the reference forests (Fig. 2a, b). In active restoration, non-pioneers represented ca. 50% of the species and individuals recorded (Fig. 2).

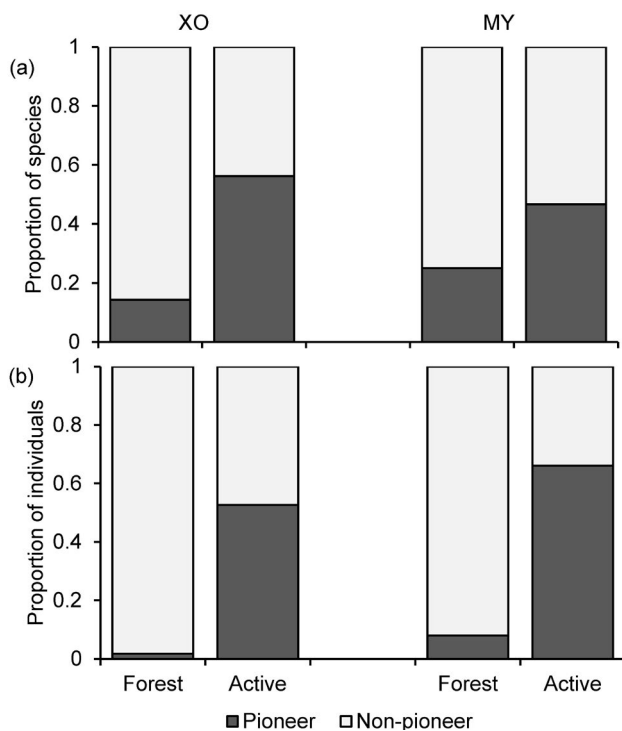


Figure 2. a) Proportion of species and b) Proportion of individuals. Tree species are classified by successional stage (pioneer and non-pioneer trees) in mature forest and 19-year-old active restoration (natural regeneration without planted trees) in XO and MY cloud forest areas of central Veracruz, Mexico.

The proportion of tree species with different seed dispersal modes was similar in forests and active restoration plantations (XO G-test = 1.63, MY G-test = 0.41, $p > 0.05$, Fig. 3a), however, the proportion of individuals was different between treatments (XO G-test = 28.85, MY G-test = 66.0, $p < 0.01$, Fig. 3b). Anemochorous, barochorous-synzoochorous and endozoochorous seed dispersal modes were represented in both active restoration and reference forests (Fig. 3). In XO, the proportion of wind-dispersed species and individuals was similar between the forest and active restoration. In MY, the proportion of endozoochorous species and individuals was similar in forest and active restoration, however the proportion of anemochorous was greater and the proportion of barochorous-synzoochorous individuals was smaller in active restoration than in forest (Fig. 3a, b).

The NMDS ordination achieved the greatest reduction in stress with a three-dimensional solution (final stress = 19.1, final instability = 0.00031, 500 iterations). The proportion of variance represented by Axis 1 and Axis 2 was 0.24 and 0.16, respectively. The Monte Carlo test indicated that the extracted axes were significantly different from those expected by chance ($p = 0.004$). NMDS analysis showed that species composition clearly differs

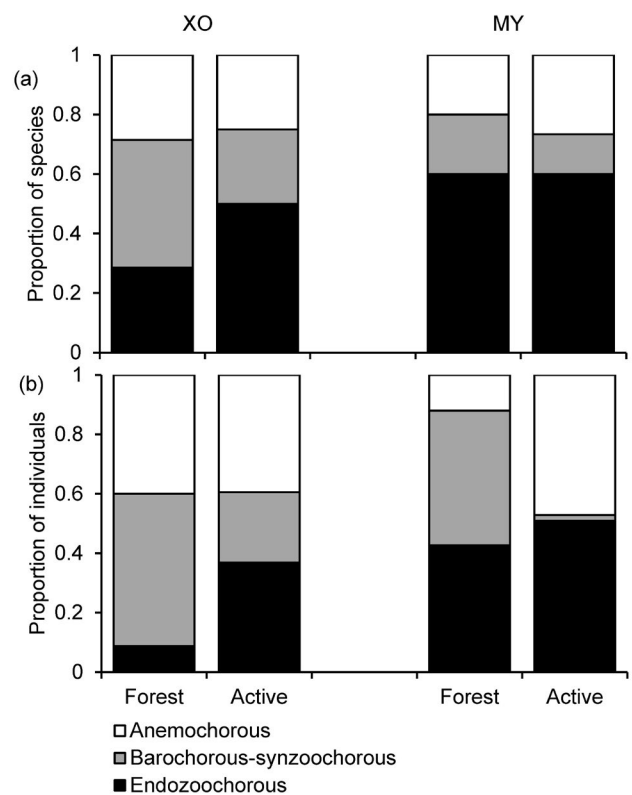


Figure 3. a) Proportion of species and b) Proportion of individuals. Tree species are classified by seed dispersal mode (anemochorous, barochorous-synzoochorous, endozoochorous) in the reference forest and 19-year-old active restoration (natural regeneration without planted trees) in XO and MY cloud forest areas of central Veracruz, Mexico.

between the XO and MY locations. In XO there is a clear trend of active restoration to merge with forest plots, whereas in MY, there is a trend separating active restoration and forest plots (Fig. 4).

Discussion

Nineteen years after establishment, the survival and growth of planted trees were relatively high in both sites. As expected, the performance of the planted tree species varied between sites, but overall they represented 36-55% of the basal area and 45-85% of the tree density of the natural regeneration of woody plants. Our results demonstrate that native tree species plantations are able to catalyze the recovery of vegetation structure and composition by directly reestablishing trees, suppressing exotic grasses and ferns, and improving site conditions, thus facilitating the recruitment of other native tree species in their understory.

The planted trees and woody vegetation that grew under the active restoration plantations had lower basal area and height values, and a higher density than the reference forest in both study sites. Similar trends have been found in the tropical forests of Brazil (Garcia *et al.*, 2016),

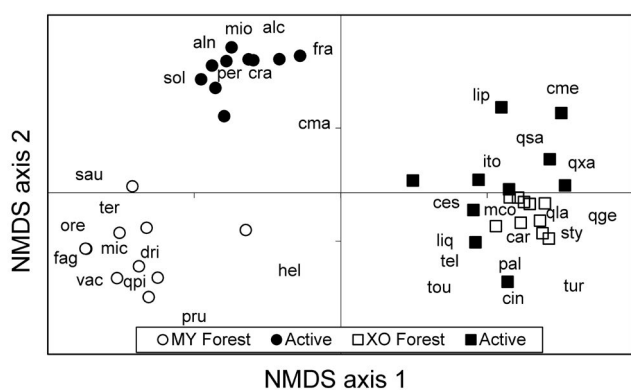


Figure 4. Nonmetric multidimensional scaling ordination for reference forest (open symbols) and 19-year-old active restoration (filled symbols) in XO and MY, Veracruz, Mexico. Tree species are: alc, *Alchornea latifolia*; aln, *Alnus jorullensis*; car, *Carpinus tropicalis*; ces, *Cestrum nocturnum*; cin, *Cinnamomum effusum*; cma, *Clethra macrophylla*; cme, *Clethra mexicana*; cra, *Crataegus mexicana*; dri, *Drimys granadensis*; fag, *Fagus grandifolia*; fra, *Frangula capreifolia*; hel, *Heliocarpus donnellsmithii*; ito, *Ilex toluhana*; lip, *Lippia myriocephala*; liq, *Liquidambar styraciflua*; mic, *Miconia glaberrima*; mio, *Miconia oligotricha*; mco, *Myrsine coriacea*; ore, *Oreopanax xalapensis*; per, *Persea americana*; pru, *Prunus samydoidea*; qge, *Quercus germana*; qla, *Q. lancifolia*; qpi, *Q. pinnatifidulosa*; qsa, *Quercus sartorii*; qxa, *Q. xalapensis*; sau, *Saurauia leuocarpa*; sol, *Solanum nigricans*; sty, *Styrax glabrescens*; tel, *Telanthophora grandifolia*; ter, *Ternstroemia sylvatica*; tou, *Tournefortia hirsutissima*; tur, *Turpinia insignis*; vac, *Vaccinium leucanthum*.

Costa Rica (Gilman *et al.*, 2016; Reid *et al.*, 2015), Puerto Rico (Ruiz-Jaen & Aide, 2005b), and for the cloud forests of Andean Ecuador (Wilson & Rhemtulla, 2016) and Mexico (Trujillo-Miranda *et al.*, 2018). Active restoration basal area represented 45-69% of that of the forest, whereas tree density in restoration plantations was 1.2 -2.1 times higher than in the reference forests. The height of our plantations is in the range of values reported for other plantations established in tropical forests (Garcia *et al.*, 2016; Trujillo-Miranda *et al.*, 2018). In relation to a chronosequence, the values of basal area, density and height in active restoration corresponded to those of a ca. 30-year-old secondary forest (Muñiz-Castro *et al.*, 2012). Still, it may take 50-80 years of recovery for forest structure to resemble that of a mature forest (Muñiz-Castro *et al.*, 2012; Garcia *et al.*, 2016).

Plant species richness is the most common measurement for assessing the recovery of diversity in active restorations (Ruiz-Jaen & Aide, 2005a; Gatica-Saavedra *et al.*, 2017). Our results demonstrate that, in terms of species richness, biodiversity was recovered in the 19-year-old active restoration plantations and fell within the range of reference forest richness. Interestingly, we observed physiognomic homogenization in the areas surrounding our plantations: without planted trees, secondary succession was slow, almost null, after 19 years, and those non-planted areas were poor in woody plants and still dominated by exotic grasses and bracken fern (personal observation). A similar trend was reported for the Ecuadorian Andes where the highest richness was recorded in cloud forest (88 species), followed by an eight-year-old plantation (44 species), and a naturally regenerating site (15 species) (Wilson & Rhemtulla, 2016). In contrast, in the tropical wet forest of Costa Rica, Gilman *et al.* (2016) found consistent richness and floristic composition recovery in five-year-old plantations (13-16 species) and passive restoration (14 species). In a Mexican cloud forest elsewhere in Veracruz, Trujillo-Miranda *et al.* (2018) reported similar tree species richness in mature forest (26 species), 21-year-old active (23 species) and passive restoration (21-26 species), but species composition differed greatly between the mature forest and the restoration sites.

Our ordination strongly suggests that forest locations have different tree species assemblages depending on elevation and correspond to upper and lower montane forests (Williams-Linera *et al.*, 2013). These results indicate that the species composition of each active restoration site was more similar to its own reference forest. We also found that tree species composition differed between the middle-aged plantations and forests but less in the lower montane than in the upper montane cloud forest.

Similar trends have been reported for other Neotropical forests (Garcia *et al.*, 2016; Wilson & Rhemtulla, 2016). In Andean Ecuador cloud forest, the species composition of naturally regenerating stems in planted sites was

different from both unplanted forests and primary forests (Wilson & Rhemtulla, 2016). In riparian Atlantic Forest, Brazil, the floristic composition and the proportions of species among guilds in restoration plantations was distinct from the set of species planted and more similar to the nearest secondary forest, but different from that of a primary forest (Suganuma *et al.*, 2014).

Planted trees favored the entry of several non-pioneer species into the plantations, therefore in active restoration, the proportion of non-pioneer species already represented ca. 50% of the trees. As expected, the proportion of tree species classified as non-pioneer was the highest in the mature reference forests. Light-demanding or pioneer woody species are associated with early successional stages, while species that are intermediate or shade-tolerant are associated with late successional stages (Muñiz-Castro *et al.*, 2012; Wilson & Rhemtulla, 2016; Trujillo-Miranda *et al.*, 2018). Although shade-tolerant forest species are still lacking in middle-aged plantations, intermediate shade-tolerant species dominate the canopy as planted trees and naturally recruited tree species in both restoration plantations.

Our middle-aged active restoration plantations were already displaying the seed dispersal syndromes recorded for mature forests, however, the proportion of individuals differed. The number of species with seed dispersal modes dependent on animals was similar in restoration plantations and forests, which indicates the presence of the fauna that maintain connectivity between different types of vegetation cover (Holl *et al.*, 2000; Suganuma *et al.*, 2014; Reid *et al.*, 2015). Similarly, in other Neotropical forests, it has been reported that active restoration treatments have a high proportion of zoochorous tree species, and unplanted sites were mainly characterized by small, anemochorous tree species (Suganuma *et al.*, 2014; Wilson & Rhemtulla, 2016). Anemochorous species are associated with early successional stages and decreased in proportion from early successional to mature forest (Suganuma *et al.*, 2014; Muñiz-Castro *et al.*, 2012). Also, the predominance of a given dispersal mode may be related to past disturbance history. Species with the barochorous dispersal syndrome in an active restoration site may be related to the presence of remnant oak trees (*Quercus xalapensis* and *Q. germana*), and *Acacia pennatula* trees that persisted from the abandoned pasture. The high proportion of anemochorous species in other active restoration sites may be related to nearby secondary forests of *Alnus jorullensis*.

Trees planted in the active restoration plantations developed a canopy, leading to the suppression of exotic grasses and bracken fern, and changing microenvironmental conditions to allow for the arrival and establishment of non-pioneer cloud forest tree species, as well as anemochorous, barochorous, and zoochorous species. Active restoration accelerated secondary succession by 30-35

years in terms of vegetation structure, and the proportions of functional groups of species. Thus, active restoration is an effective means of promoting the recovery of tropical montane cloud forest under scenarios of an abandoned pasture and arrested succession. In conclusion, the ecological restoration of Mexican cloud forest is considered a priority to both conserve biodiversity and maintain key ecosystem services (Tobón *et al.*, 2017). Our results are relevant for the ambitious goals that Mexico has set in both international agreements (*e.g.*, the Aichi Target of restoring 15% degraded lands) and national strategies (the Mexican Strategy on Biodiversity and Action Plan 2016-2030; Tobón *et al.*, 2017). However, rather than contributing directly to the urgent short-term restoration goals established in these efforts, our results help to clarify the true timescales over which restoration occurs, and to highlight the importance of long-term studies with continuous monitoring to improve restoration techniques and thus maximize the recovery of the ecosystem functions and services provided by TMCF.

Acknowledgments

We thank Javier Tolome and Maryxu Peralta for help in the field, and Silvia H. Salas and Claudia Gallardo for help identifying plant specimens. We are grateful to José Ramos Melo and Antonio Casazza for permission to establish active restoration plantations in their properties.

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