Live Fences as Refuges of Wild and Useful Plant Diversity: Their Drivers and Structure in Five Elevation Contrast Sites of Veracruz, Mexico

Authors: Zamora Pedraza, Gregoria, Avendaño-Reyes, Sergio, Coates, Rosamond, Gómez Díaz, Jorge Antonio, Lascurain, Maite, et al.

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Live Fences as Refuges of Wild and Useful **Plant Diversity: Their Drivers and Structure in Five Elevation Contrast Sites of Veracruz**, Mexico

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Gregoria Zamora Pedraza¹, Sergio Avendaño-Reyes², Rosamond Coates³, Jorge Antonio Gómez Díaz¹, Maite Lascurain⁴, Graciela García-Guzmán⁵, and Juan Carlos López-Acosta¹ 💿

Abstract

Background and Research: One noteworthy element found throughout the tropical anthropogenic mosaic is the live fence, which is established within agricultural matrices and its structure within the landscape retains ecological processes, but few are recognized as elements of biological and cultural conservation.

Methods: In this study, we have researched plant diversity and anthropic management of live fences in five sites surrounded by contrasting vegetation references: Tropical evergreen forest; tropical deciduous forest; cloud forest; and pine-oak and pine forests. We recorded the type of management by interviews with peasants. We established thirty 2 × 50 m transects within each site and sampled two strata: trees and saplings. Also, we documented seed dispersal mechanism, life form, local use, and origin of each species. Importance Value Index and diversity metrics were estimated for each site.

Results: 253 plant species were registered (181 genera/74 families). While fences associated with the tropical deciduous forest showed the greatest species richness (109 species), the pine forest fences showed the lowest richness (21 species). Zoochory was the main type of seed dispersal mechanism.

Conclusions: Independent to the site and the altitude, the configuration of living fences is structured by three processes: the selection of the initial trees, the availability of the arrival of zoochory species, and the tolerance of the owners for the plant species.

Implications for Conservation: Based on our results, live fences can be considered important tools for landscape management in Mexico.

Keywords

life fences, plant conservation, tropical evergreen forest, tropical deciduous forest, cloud forest, pine-oak and pine forests, plant diversity, useful species, altitudinal contrast, Mexico

¹Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Mexico ²Herbario XAL, Instituto de Ecología, A.C., Xalapa, Mexico

³Estacion de Biologia Tropical Los Tuxtlas, Universidad Nacional Autonoma de Mexico Instituto de Biologia, Mexico D.F., Mexico ⁴Ambiente y Sustentabilidad, Instituto de Ecologia, A.C., Xalapa, Mexico

⁵Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de Mexico, Mexico

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Corresponding Author:

Juan Carlos Lopez-Acosta, Centro de Investigaciones Tropicales, Universidad Veracruzana, José María Morelos 44, Zona Centro, Xalapa 91000, Mexico. Email: carlolopez@uv.mx



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Introduction

As a result of the negative impact caused by human activities, the natural tropical landscape has been transformed into a matrix of grasslands or annual crops surrounding forest remnants in different states of conservation, live fences, and isolated trees (Dirzo et al., 2009; Harvey et al., 2005). These elements have the potential to harbor biological diversity and pose a contemporary challenge for conservation, management, and restoration of (Challenger & Dirzo, 2009).

One of the characteristic elements of this anthropogenic landscape is the live fence scenario which is a linear system of woody trees used by the local peasants to divide parcels of land destined for different uses such as pastureland, cropland, and in some instances patches of the forest (Harvey et al., 2005). These live fences are created by using the large branches or trunks of native woody tree species and sometimes are combined with wooden or concrete fence posts. Generally, persistent trees with rapid foliage regeneration are used; however, shrubs and occasionally herbaceous species are also included. These fences are established in diverse areas, with different elevations and ecological characteristics, and are immersed in a wide diversity of cultures with different histories of land use and agricultural production (Budowski, 1987). The present structural and appropriation peculiarities of the neotropical landscape that differentiate them from the "hedgerows," common in temperate zones in western Europe (Le Coeur et al., 2002).

Empirical evidence documents that live fences have great value from an ecological perspective: they maintain biodiversity, retain soil to prevent its degradation and erosion by water or wind (Tamayo-Chim & Orellana, 2007), influence animal movement patterns, contribute to the physical connectivity of the landscape, and also serve as corridors between patches of isolated forests (Estrada & Coates-Estrada, 2001; Harvey et al., 2004). Previous studies have shown that they also function as refuge areas, ecological habitats, and passageways for certain organisms (Bennett, 1990; Guevara & Laborde, 1993; Guevara et al., 1998; Johnson & Beck, 1988; Millán de la Peña et al., 2003) such as plants, insects, birds, and small mammals (Burel, 1996). Under these conditions live fences have become important systems of study since they function as potential sites to harbor useful and native species within livestock matrices (Ruiz-Guerra et al., 2014). In addition, they can form synergies with other management systems. For example, isolated trees within pasturelands serve as refuge areas for important seed dispersers, which in turn promote natural succession processes (Guevara et al., 1992). Their structure is dynamic, may include different successional stages of vegetation and composition, and supply food for birds and some mammals (Molano et al., 2003).

In addition, live fences increase the flow of propagules necessary for the maintenance of genetic variability within the landscape (Harvey et al., 2008; Hilty & Merenlender, 2004). It has been shown that live fences also increase land

productivity and diversification of products on livestock farms, and are also important sources of fodder, firewood, timber, and fruit (Harvey et al., 2003; Tobar and Ibrahim, 2010). Therefore, the zoochorous plants should be the ones that dominate the structure of the living fences. Beyond the ecological processes, these fences are man-made elements and commonly managed by the local peasants (Hernández et al., 2001), they are exposed to different environmental conditions and local management practices, and therefore they vary in size, structure, composition, and function (González-Valdivia et al., 2012; Harvey et al., 2005). Furthermore, their physiognomy depends on the region, the dynamics within the landscape, and the preferences of the peasants (for tolerance, protection, or promotion of particular species (Moreno-Calles et al., 2010; Rendón-Sandoval et al., 2020), seed availability, the history of land use, the production systems, land parcel size, pasture management, and adjacent vegetation (Burel, 1996; Ibrahim et al., 2007). A report by Budowski (1987) in Central America showed that live fences were established with multipurpose trees that had timber value, harvestable fruit production, shade, and fodder attributes (Barrance et al., 2003; Hernández & Simón, 1993) and mainly favor livestock (Ivory, 1990). Regardless of being common elements throughout the Neotropical landscape, there is little qualitative information on aspects such as the plant diversity they host, the type of management as well as, the potential use of the flora (Avendaño Reyes & Acosta Rosado, 2000; Ruiz-Guerra et al., 2014). Given this panorama, it is necessary to investigate the current use and management of plant species established along the live fences, as well as their retention of floristic diversity in landscapes dominated by anthropogenic use with some adjacent remnants of the natural ecosystems.

The present study is focused on analyzing the structure and composition of live fence vegetation, as well as the mechanisms that could favor plant fitness or recruitment success, such as plant dispersal syndromes (for example, zoochory, anemochory, and autochory), and life forms (tree, shrub, liana, herbs). These variables allowed us to determine recruitment vectors and permanence of plant species in the fences. We also registered the local reference vegetation affinity (native or introduced), which indicates the contribution of the fences to the retention of the plant diversity of the original system.

Other factors that can shape the structure of living fences found in the tropics are differences in environmental conditions. This study was carried out in five areas characterized by a high environmental heterogeneity (natural and anthropogenic), elevation gradient, and different local management practices as strong transformation drivers within the state of Veracruz, Mexico. In particular, the elevational gradient found in this area presents a unique opportunity to test hypotheses related to the influence of abiotic factors on the composition of species. This gradient begins at sea level and reaches 4282 m a.s.l. This area is located between two biogeographical regions (Nearctic and Neotropic), and within only 81 km there are four climate types and five forest biomes present (Carvajal Hernández et al., 2020).

The main aim was to identify the retention potential of floristic diversity, as well as to list some management practices and to compare the species composition along five relevant ecosystems in the Neotropics associated with an altitudinal gradient. Our working hypothesis is that live fences will have a configuration dominated by useful species, which arrive through zoochory dispersal and are tolerated and promoted by the owners. This pattern must be constant regardless of the reference ecosystem and altitude. Therefore, living fences form a system with high cultural and ecological value, serving as a safeguard for relevant species typical of native forests and increasing the connectivity of the landscape.

Materials and Methods

Selection and Location of Sampling Sites

The study sites were selected based on the physiognomic characteristics such as the type of reference vegetation along an elevational gradient (from 10 to 3500 m a.s.l.) and current land use practice. A centroid surrounded by the land uses of each region was placed. Then, a circular buffer of a 5 km radius was created where we had placed the sampling sites for live fences. A distance with reference vegetation (>300 m) was maintained to reduce a possible nearby influence on the plant richness of the fences (Figure 1; Table 1).

Los Tuxtlas: The sampling sites were located between the communities of Balzapote and Montepío (18° 36.53' N and

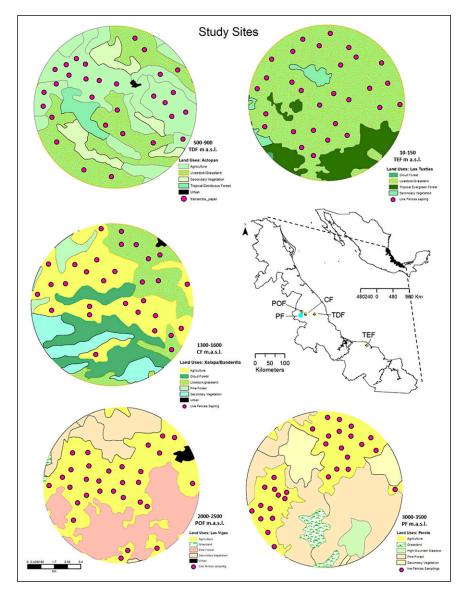


Figure 1. Sampling sites of live fences in five different reference vegetation. In each ecosystem, 30 linear transects of 50 m \times 2 m were sampled along the live fences.

| Sampling sites | m a.s.l. | Vegetation reference |
|----------------------------|-----------|---------------------------------|
| Los Tuxtlas | 10–150 | Tropical evergreen forest (TEF) |
| Actopan–Naolinco | 500–900 | Tropical deciduous forest (TDF) |
| Tlalnelhuayocan–Banderilla | 1300-1600 | Cloud forest (CF) |
| Las Vigas de Ramírez | 2000–2500 | Pine–oak forest (POF) |
| Perote | 3000–3500 | Pine forest (PF) |

Table I. Sampling locations, altitudinal ranges, and reference vegetation according to Rzedowski (1978).

95° 4.82′ W, and 18° 40.35′ N and 95° 9.04′ W: 10–150 m a.s.l.). Fragmentation in this region is very high as a result of activities related to livestock production. In addition, patches of secondary vegetation are found in different successional stages. The main vegetation type in the area is tropical evergreen forest (TEF) (Rzedowski, 1978).

Actopan–Naolinco: This is in the center of Veracruz, at the bottom of the flat valley of the upper-middle basin of the Actopan River (19° 31' and 19° 37' N, 96° 41' and 96° 54' W; 500–900 m a.s.l.) (Castillo-Campos et al., 2007). The main productive activities in the area are livestock production and sugar cane crops (*Saccharum officinarum*), chayote (*Sechium edule*), and coffee (*Coffea* spp.). The main vegetation type in the area is the tropical deciduous forest (TDF) (Rzedowski, 1978).

Tlalnelhuayocan–Banderilla: Sampling was carried out in the municipalities of Tlalnelhuayocan (19° 33.74' N and 96° 58.71' W) and Banderilla (19° 35.23' N and 96° 56.15' W; 1300–1600 m a.s.l.). The type of vegetation present in both communities is cloud forest (CF) (Rzedowski, 1978). The main productive activities in the area include livestock production, corn (*Zea mays*), and coffee (*Coffea* spp.) crops.

Las Vigas de Ramírez: The sampling sites were established in the municipality of Las Vigas, (19° 37.8' N and 97° 05.83' W; 2000–2500 m a.s.l.). The vegetation in the area is pine–oak forest (POF) (Rzedowski, 1978), mainly located on the hills of volcanic and sedimentary origin of the "altiplano," with shallow and rocky soils (Cházaro Basáñez, 1992). Productivity in this region depends on raising livestock, corn (*Zea mays*), and potato (*Solanum* spp.) crops.

Perote: The sampling site was located in El Conejo community (19° 33' 56.70" N and 97° 14' 35.26" W; 3000– 3500 m a.s.l.). The region is characterized by timber plantations, potato (*Solanum* spp.), and broad bean crops (*Vicia faba*). Goats and sheep predominate in the area. The main vegetation is pine forest (PF) (Rzedowski, 1978).

Analysis of Plant Diversity Associated with Live Fences

In each site, we selected 30 linear transects of 50×2 m (total 300 m²) using the live fence as the central axis for each transect. These dimensions for each transect have been commonly used for floristic studies in the neotropics (Gentry, 1982). All transect groups were selected in the same altitudinal range inside the buffer. Each transect was placed

independently from each other and included all the physiognomic heterogeneity of the fences. In all cases, the dominant land uses were agriculture and livestock.

In each transect we distinguished two plant strata: all individuals with a diameter at breast height (DBH) ≥ 1 cm were included among the canopy trees (CT), and individuals with a diameter <1 cm and a height >30 cm were considered as shrubs and saplings (SS), this group being an indicator of species recruitment in the fences. Using these data, the Importance Value Index (IV) (Lamprecht, 1990) was calculated based on the values of density (DeR), frequency (FR), and dominance (DoR) for the CT group. Density (DeR) and frequency (FR) were also calculated for the SS group. We collected specimens of all surveyed plants, which were duly processed, identified by a botanist specialist (Sergio Avendaño), and then deposited in the XAL Herbarium of the Institute of Ecology, A.C. (INECOL).

To evaluate the intensity of our sampling effort, cumulative curves were generated for each group of transects using the EstimateS statistical program EstimateS 9.1.0 and the potential deficit evaluated using Chao-1 estimators (Chao et al., 2009). The alpha (α) diversity metrics were calculated by all plants and for each stratum and site, we calculated the number of individuals, richness, Shannon index (entropy), and Buzas and Gibson's evenness: e^{H/S} (H by natural logarithm). To estimate sample variability for all diversities metrics, we performed bootstrap resampling to build confidence bounds (Solow, 1989) by applying a 10,000-times sorting the order of the transects using the software PAST.

For each site and strata, we estimated the effective number of species (also called Hill numbers) used q exponent 0, 1, and 2, exploring the sensibility of the estimator to the abundance relative of each species. q = 0 counts species equally without regard to their relative abundances, q = 1counts individuals equally and thus weigh species in proportion to their abundances, and q = 2 excludes all except the dominant species.

For beta diversity, we compared N sets of species relative abundances by site, then communities are equally weighted using the index U_{2N} (q = 2, N-community equal-weight regional overlap index) and C_{2N} (q = 2, N-community Morisita-Horn similarity index). The measures of q = 2 are mainly sensitive to dominant species. The results for q = 2emphasize the resemblance among the more abundant species. To test the relationship between diversity and elevation, we performed a simple linear relationship, taking as an independent variable the mean range of each altitude and the number of records for each variable (species, genus, and family) by absolute records, uses, and type of dispersal syndrome by proportional/total records, as a dependent variable. We performed this procedure using the statistical package Entropart (Marcon & Hérault, 2015) and SpadeR (Chao et al., 2016) in R Development Core Team Ver. 4.1.2.

Dispersal Syndromes/Life Forms

We reviewed specialized botanical literature and fruits/seed characteristics for each species. As well, we documented their seed dispersal syndromes as zoochory, anemochory, autochory, barochory, or hydrochory. Moreover, we registered their life form (tree, shrub, liana, and herb), and origin in terms of the association with the reference vegetation and whether the species was introduced/exotic, and its uses by conducting specialized literature searches/interviews. Both variables: dispersal syndromes and the life forms were evaluated according to their frequency in each site by non-parametric association tests.

Management and Use of Plants into Live Fences

To have a complete overview of the characteristics and importance of live fences in each of the study sites, 20 semistructured interviews were conducted with consenting peasants. For each study site, we located the property owners with knowledge of the local history, live fence practices, and useful plants. The study sites were selected according to the type of ecosystem, altitude, climate, and vegetation. In total, 20 interviews were conducted. In this case, no questionnaires were applied to the owners of the live fences (all Spanish speakers), because several of them cannot read and write. All interviews were verbal. The researchers followed the International Society of Ethnobiology (Ethnobiology, 2006). Before we started each survey, we presented the project aims, acquired consent to participate, and use the information confidentially. Twenty interviews were conducted, 19 were men and one woman, between the ages of 60 and 70 years. The local people were mestizo peasants, involved in subsistence farming and livestock activities. We asked detailed questions about the management practices (pruning, tree replacement, and sapling clearing) and the local use of the species found in the live fences.

Results

Sampling Completeness

The validation of the sampling effort using the Chao-1 estimator showed that, for plants in the CT and in the SS group, in live fences adjacent to the TEF showed a deficit of 17% (96 vs. 80). While in the fences associated with TDF, CF, POF, and PF values predicted by Chao-1 are closer to those observed in the field and with deficits between 12% and 7% (Table 2).

For the shrubs and saplings group, the highest sampling deficit (12%) is recorded in the fences associated with the TEF, the estimator predicts that 66 species should have been found, but the estimator observed only 58. Data obtained from the sapling vegetation of the fences associated with the other types of vegetation (TDF, CF, and PF), indicated a completeness of 100% obtained by finding all the species predicted by the estimator.

Table 2. Sampling effort and diversity metrics of vegetation in live fences in each ecosystem and strata. For diversity metrics with different superindices (a,b,c,d) indicate statistically contrasting pairs ($p \le .05$).

| Ecosystems reference | Richness S | Families/genus | Chao-I (value/deficit %) | Individuals | ٩l | Shannon H | Evenness eH/S |
|----------------------|------------------|----------------|--------------------------|--------------------|------|-------------------|--------------------|
| TEF | 80 ^ª | 30/62 | 96 (17%) | 2671ª | 21.5 | 3.08ª | 0.27 ^a |
| TDF | ۱09 ^ь | 38/82 | 117 (7%) | ۱67۱ ^ь | 27.8 | 3.35 ^b | 0.26ª |
| CF | 69 [°] | 46/60 | 72 (4%) | 2171° | 33.3 | 3.52 ^c | 0.48 ^b |
| POF | 21 ^d | 14/19 | 24 (12%) | 246 I ^d | 7.8 | 2.06 ^d | 0.37 ^c |
| PF | 22 ^d | oct-19 | 26 (12%) | 1898 ^e | 9.1 | 2.2 ^e | 0.39 ^c |
| Canopy Trees | | | | | | | |
| TEF | 57 ^a | 24/44 | 78 (27%) | 1187 ^a | 9.4 | 2.26 ^ª | 0.168ª |
| TDF | 91 ^b | 34/73 | 109 (17%) | 798 ^ь | 21.2 | 3.1 ^b | 0.248 ^c |
| CF | 61° | 43/55 | 65 (6%) | 820 ^c | 21.5 | 3.1 ^b | 0.366 ^b |
| POF | 19 ^d | 13/17 | 29 (34%) | 1004 ^d | 8.5 | 2.14 ^a | 0.450 ^d |
| PF | 21 ^d | sep-18 | 26 (19%) | 624 ^e | 9.9 | 2.3ª | 0.478 ^d |
| Shrubs and saplings | | | | | | | |
| TEF | 58ª | 26/46 | 66 (12%) | 1484 ^a | 23 | 3.02 ^ª | 0.3543ª |
| TDF | 63 ª | 29/55 | 63 (0%) | 896 ^b | 23 | 2.93 ^b | 0.298ª |
| CF | 54 ^a | 35/46 | 54 (0%) | 1352° | 27 | 3.28 ^c | 0.494 ^b |
| POF | 16 ^b | dic-16 | 16 (0%) | 1457 ^d | 7 | I.86 ^d | 0.403 ^c |
| PF | 20 ^c | sep-17 | 20 (0%) | 1388 ^e | 8 | 2.02 ^e | 0.377 ^a |

Floristic Data

In general, alpha diversity (α) was recorded in a total of 253 species of plants, belonging to 74 families and 181 genera, in 150 live fences of 50 × 2 m each corresponding to 1.5 ha (15,000 m² total).

The fences associated with the TDF registered the highest species richness (109), grouped into 38 families and 92 genera. In fences associated with CF, 69 species (46 families and 60 genera) were documented. Live fences established at higher elevations had lower species richness, as observed for the POF and PF, where only 21 and 22 species were recorded, respectively, its contracting richness was not statistically significant but distinguishable in individuals, using the Shannon Index (Appendix A; Table 2). The live fences located in the CF were found to be more diverse Shannon Index H = 3.5. We documented a total of 69 species, which represented 2171 individuals. Fences near TDF (H = 3) and TEF (H = 3)registered intermediate diversity values. The fences with the lowest values of species diversity were those adjacent to the POF (H = 2) and PF (H = 2.2). When the H values of the live fences were compared among the distinct ecosystems, all areas were significantly different (p < .05). Regarding uniformity, the CF registered the highest value above the other systems (0.489) and the lowest value was registered in TD (Table 2). In terms of effective number of species, in accordance with richness, we found that q_0 presented the highest value in TDF. However, both for q_1 and q_2 the highest values were registered in CF, in q_1 the lowest value was presented by POF while in q_2 it was registered in PF (Figure 2).

For the canopy trees (CT), we found that the fences associated with the TDF had the highest number of species. However, we found that fences adjacent to the TEF and POF held the higher number of adult individuals (1187 and 1004 individuals respectively). Fences near the PF had the lowest number of species (21) and individuals (624) represented by only 9 genera and 18 families (Table 2). Statistical comparison of these diversity metrics showed that all sites differed from each other in the number of individuals. For the Shannon index, we find that TDF and CF have the highest values (3.1 both) and they differ from TEF, POF, and PF are statistically indistinguishable from each other (Table 2). For uniformity, the highest values were presented by POF and PF with significantly higher values than other systems. In terms of effective number of TDF species presents the highest value for q_0 , in q_1 TDF and CF present values of 21 each and higher than the others, for q_2 the CF again presents the highest value.

Regarding the SS category, the fences adjacent to the TDF held the greatest number of species. In contrast, only 20 and 16 species were recorded in the fences associated with the PF and POF ecosystems respectively (Table 2). The fences associated with TDF and CF were the most diverse (H = 3.2) in contrast, those associated with POF were the least diverse (H = 1.86) in terms of the number of individuals with >1 cm DBH. The fences located adjacent to tropical communities (TEF and TDF) had less evenness while the fences near CF and POF communities showed the highest (Table 2). When we compared the H values of the different ecosystems, we found significant differences in all cases CF>TEF>TDF>PF>POF (Table 2). The effective number of TDF species has the highest value for q0, in q1 CF and TEF the highest value (23 each) and the lower POF, for q^2 , CF again the highest value, but now together with TEF the lowest value was recorded in PF (Figure 2).

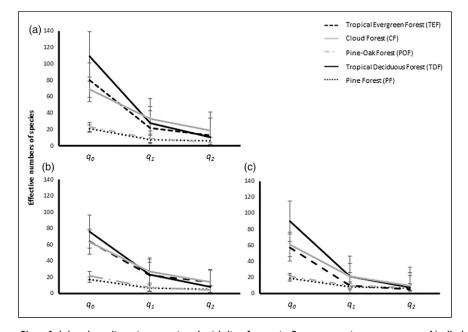


Figure 2. Diversity profiles of alpha plant diversity associated with live fences in five contrasting ecosystems: A) all plants, B) sapling plants, and C) canopy trees. Error bars indicate 95% confidence intervals.

For beta diversity, the estimators indicated low similarity values between the different sites with an average value of $C_{25}(q_2, \text{Morisita-Horn}) = 0.127$ (S.E. 1275), the most similar pairs of sites were TEF and TDF ($C_{22}0.38$) PF and POF (C_{22} 0.57). In terms of regional overlap, we had a relatively low average value of $U_{2,5}(q_2 \text{ Regional overlap}) = 0.18$ (S.E. 027), and the most similar pairs of sites were again TEF and TEF ($C_{22}0.55$) y PF and POF ($C_{22}0.73$).

Influence of Elevation on Species Diversity

We found a negative relationship between the increase in altitude with the decrease of species and genera and of the plants registered in the live fences. The slope is steeper for species and genus R = 0.73 (F = 5.7, p = .01) and R = 0.67(F = 5.19, p = .0139) respectively, and not significant for family (Figure 3).

Importance Value Index (IVI) of Live Fences/Reference Vegetation

Tropical Evergreen Forest. The species with the highest IVI due to its high dominance, frequency, and relative abundance was *Bursera simaruba* with 82% of the individuals recorded, followed by *Jatropha curcas* (31.6%), *Gliricidia sepium* (29%) of the total IVI. These three species together accounted for 144% of the IVI and were the most important in terms of the number of individuals. A total of 58 plant species in the SS category were registered. The three outstanding species for IVI, both in abundance and frequency, were *Vachellia cornigera* (27.5%), *Tabernaemontana alba* (22%), and *Eugenia capuli* (16%). IVI values between 16% and 7% were documented for the following species: *Eupatorium* sp., *Cupania dentata*, *Psidium guajava*, and *Eugenia* sp. The above seven species together reached a total IVI of 100% (Figure 4).

Tropical Deciduous Forest (TDF). Once again due to its high dominance, frequency, and relative abundance we found that B. simaruba (80%) had the highest IVI value. Whereas Spondias purpurea (40%) due to its relative abundance (19.6%) and S. mombin (17.5%) IVI value for being dominant (9.6%). These three species accounted for 137.5% of the total IVI values. Other species such as Opuntia dejecta (12), Ximenia americana (6), Cedrela odorata (8), and Acanthocereus tetragonus (6) had IVI values that ranged between 12% and 6%. Sixty-three species of plants were registered in the SS category. Of these O. dejecta stands out with the highest IVI value (46%) due to its high relative abundance (46.2%), followed in abundance and frequency by A. tetragonus (16%) and B. simaruba (14%). These last three species accounted for 76% of the total IVI value. Finally, four other species V. cornigera (9), Cestrum tomentosum (9) Acacia farnesiana (7), and C. dumetorum (5%) contributed with IVI values between 9% and 5% (Figure 4).

Cloud Forest (CF). We found that the most important species in this ecosystem was *Yucca gigantea*, which stood out with 56% of total IVI value due to its high abundance (25%), frequency (9%),

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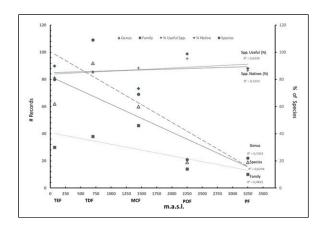


Figure 3. Total number of families, genus, and species per reference sites (records by level, y-axis left) and 189 the elevational gradient (m.a.s.l.). Proportion of useful plants and zoochory strategies represent in each elevation point (records by level, y-axis right).

and relative dominance (22%). Next, we registered Erythrina americana, which had a 37% IVI value due to its relative dominance (21%) and was followed by B. simaruba which represented 27% of the IVI value due to its relative abundance (13.6%). These three main species represented a total IVI value of 120%. Other species such as Acacia pennatula (15), Platanus mexicana (13), C. tomentosum (11), and Liquidambar styraciflua (9) presented values between 15% and 9% of the IVI. We registered a total of 54 species for the SS vegetation (<1 cm DBH; > 30 cm height) where Piper auritum was notable with 30.5% of the total IVI value due to its high relative abundance (23%). Similar values for frequency and abundance were attained for Solanum ferrugineum with 12.5% and followed by Rubus adenotrichos with 10% of total IVI. Combined, these three species reach 53% of the total IVI. The species with the lowest contribution to IVI values were Malvaviscus arboreus (9%), Quercus xalapensis (9%), Myrsine coriacea (8%), and Cestrum tomentosum (8%) (Figure 4).

Pine-Oak Forest (POF). Here, Agave salmiana turned out to be the species with the highest IVI value with 81%, mostly due to its relative abundance (29%) and dominance (41%). Next was Prunus serotina with an IVI value of 39% for its similar abundance and frequency (15%). These two species together summed up 120% of total IVI (300). Several other species showed intermediate values, and these were Baccharis conferta (30), Alnus jorullensis (30), Cupressus lusitanica (26), Barkleyanthus sp. (23), and Pinus ayacahuite (15) whose values fluctuate between 30% and 15% of the total IVI. Regarding the SS vegetation, 16 species were registered, of which Prunus serotina was the most important with an IVI value of 47%, due to its dominance and frequency throughout all sampling sites. Secondly, we found Baccharis conferta to have an IVI value of 39%. These two species represented 86% of the total IVI. Similar values of importance were documented for A. salmiana and B.

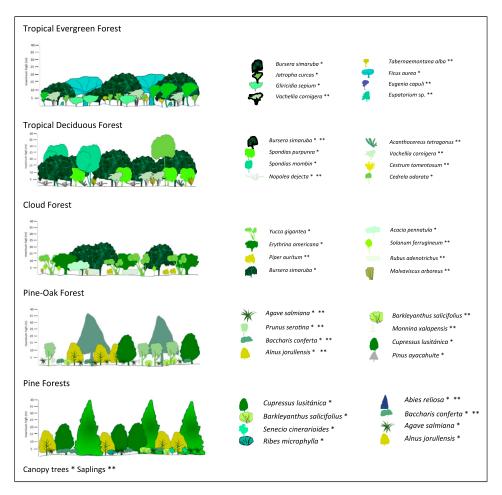


Figure 4. Graphical descriptions of structure in live fences in five contrasting ecosystems.

salicifolius with 33% and 34% of IVI, respectively. *Monnina xalapensis* showed an IVI of 17%, while two other species *A. jorullensis* and *Ribes affine* registered 6% and 5% of IVI (Figure 4).

Pine Forest (PF). One species, Abies religiosa presented an IVI value of 50% given its dominance, abundance, and relative frequency. Secondly, Baccharis conferta registered a high number of individuals (147) and contributed to 44% of the IVI value. These two species alone accounted for 94% of total IVI. Several tree species such as Alnus jorullensis (31%), Cupressus lusitanica (27.5%), and Pinus pseudostrobus (26%) presented intermediate IVI values. Two shrub species Barklevanthus salicifolius and Senecio cinerarioides registered 15% and 16% of the total IVI. We found a total of 20 species in the SS category. In this category and due to its high number of individuals (625) recorded, as well as being present in most of the sampled transects (26), Baccharis conferta accounted for 67% of the total IVI value. The following species B. salicifolius (22%), Senecio cinerarioides (17%), Ribes microphyllum (15%), Abies religiosa (14%), and Stevia monardifolia (10%) contributed to 153% of the total IVI value (Figure 4).

Dispersal Syndromes

In general, the most dominant dispersal syndrome for adult plants (>1 cm DBH) found in the live fences of four ecosystems was zoochory which presented the following frequencies (TEF = 57%, TDF = 78%, POF = 54%, and CF = 43%). On the other hand, we found that dispersal by ane-mochory was predominate in the fences established in the PF (74%; $X^2 = 362.34$, p < .05, DF = 16).

In the case of the SS plants (<1 cm DBH; > 30 cm height), zoochory was once again dominant in four ecosystems (TEF = 91%, TDF = 65%, CF = 77%, and POF = 55%). A secondary dispersal type was the autochory which was present in all live fences but with values of less than 20% per ecosystem (X2 = 214.616, p < .05, DF = 16; Table 3).

On the other hand, for the proportion of species dispersed by animals (zoochory) we did not find any relationship with altitude, registering means of 87.04% (D.E: 9) (Table 3).

Life Forms

The tree life form was the most represented for adult plants (>1 cm DBH), and it was characteristic to all fences in all the

9

| | | Dispersal syndromes | | | | | |
|------------|------------|---------------------|------------|-----------|-----------|------------|--|
| Ecosystems | Vegetation | Zoochory | Anemochory | Autochory | Barochory | Hydrochory | |
| TEF | СТ | 57/678 | 1/12 | 0 | 41/489 | 1/8 | |
| | SS | 91/213 | 5/12 | 0 | 3/8 | 1/1 | |
| TDF | СТ | 78/623 | 13/103 | 9/72 | 0 | 0 | |
| | SS | 65/106 | 15/24 | 20/33 | 0 | 0 | |
| CF | СТ | 43/353 | 13/109 | 37/303 | 7/55 | 0 | |
| | SS | 77/172 | 13/28 | 4/10 | 6/13 | 0 | |
| POF | СТ | 54/540 | 35/348 | 10/115 | 1/1 | 0 | |
| | SS | 55/60 | 43/49 | 43,892 | 11 | 0 | |
| PF | СТ | 11/68 | 74/465 | 15/91 | 0 | 0 | |
| | SS | 24/28 | 75/89 | 1/2 | 0 | 0 | |

Table 3. Percentages and absolute values of dispersal syndromes for canopy trees (CT) and shrubs and saplings (SS) plants in the live fences per ecosystem (percentages/number de individuals are indicated).

sampled ecosystems ($X^2 = 143.75$, p < .05, DF = 12). It was also evident that shrubs were also dominate in the fences established in the different ecosystems, but these showed lower percentages (TEF = 34%, TDF = 18%, CF = 20%, POF = 30%, and PF = 46%).

For the shrubs and saplings category, (<1 cm DBH; > 30 cm height) we found that the life form most associated with the live fences were shrubs (TDF = 46%, CF = 54%, POF = 52% and PF = 63%). However, in the TEF, we found more trees (63%) than shrubs. Vines were associated more with the fences of the TDF (15%; X^2 = 88.56, p < .05, DF = 12; Table 4).

Origin of Plants (Native vs. Introduced)

Among the sampling sites for all the live fences in the different ecosystems the adult plants registered were mostly native species with high frequency values of >80% (TEF = 93%, TDF = 87%, CF = 80%, POF = 99%, and PF = 90%). We only found minimum percentages of introduced plants in the fences adjacent to the five ecosystems (TEF = 2%, TDF = 1%, CF = 3% POF = 1%, and PF = 1%).

In the case of the SS plants (<1 cm DBH; > 30 cm height), native plant species in the fences were dominant in all five ecosystems (TEF = 77%, TDF = 76%, CF = 51%, POF = 96%, PF = 76%; X2 = 16.77, p < .05, DF = 8; Table 5).

Some of the noteworthy introduced species were citrus plants such as oranges (*Citrus sinensis* and lemons *Citrus limon*). We also recorded fruit trees such as mango (*Mangifera indica*), jackfruit tree (*Artocarpus heterophyllus*), Japanese Medlar (*Eriobotrya japonica*), apples (*Malus domestica*), and plums (*Prunus domestica*), in addition to coffee plants (*Coffea arabica*) (see Appendix A).

Uses for Live Fence Plants

We documented CT species used for medicinal purposes in all five ecosystems ($X^2 = 386$, p < .05, DF = 36), where they reached values of >40% (TEF = 43%, TDF = 68%, CF = 47%,

 Table 4.
 Percentages and absolute values of life forms of adult and shrubs and saplings plants in the live fences per ecosystem (percentages/number de individuals are indicated).

| | | Life form | | | | |
|-----------|------------|-----------|--------|-------|--------|--|
| Ecosystem | Vegetation | Tree | Shrub | Liana | Herbs | |
| TEF | СТ | 66/783 | 34/402 | 0/2 | 0 | |
| | SS | 63/148 | 36/85 | 1/1 | 0 | |
| TDF | СТ | 80/643 | 18/142 | 2/13 | 0 | |
| | SS | 39/64 | 46/75 | 15/24 | 0 | |
| CF | СТ | 80/655 | 20/165 | 0 | 0 | |
| | SS | 41/92 | 54/120 | 5/11 | 0 | |
| POF | СТ | 41/412 | 30/304 | 0 | 29/288 | |
| | SS | 33/37 | 52/59 | 0 | 15/17 | |
| PF | СТ | 51/316 | 46/290 | 0 | 3/18 | |
| | SS | 26/31 | 63/75 | 0 | 11/13 | |

Table 5. Percentages and absolute values of native and introduced plants category: Canopy tree (CT), and shrubs and saplings (SS) in the live fences per ecosystem (percentages/number de individuals are indicated).

| Ecosystem | Vegetation | Native | Introduced | |
|-----------|------------|---------|------------|--|
| TEF | СТ | 93/1098 | 2/25 | |
| | SS | 77/179 | 7/15 | |
| TDF | СТ | 87/696 | 1/6 | |
| | SS | 76/124 | 0 | |
| CF | СТ | 80/65 I | 3/29 | |
| | SS | 51/113 | 2/4 | |
| POF | СТ | 99/995 | 1/9 | |
| | SS | 96/108 | 3/4 | |
| PF | СТ | 90/564 | 0 | |
| | SS | 76/90 | 0 | |

POF = 45%, and PF = 50%). On the other hand, the fences in the CF held several edible plants (30%), whereas in the fences surrounding the TEF vegetation the use of plants for fuel was the most important (39%) (Table 6).

| Ecosystem | Local name | Species | Uses | Propagation method |
|-----------|-------------|--------------------------------------|---|-----------------------------|
| TEF | Cocuite | Gliricidia sepium | Construction, timber, edible, forage, firewood | Stakes |
| | Mulato | Bursera simaruba | Timber | Stakes |
| | Piñón | Jatropha curcas | Timber | Stakes |
| TDF | Ciruelas | Spondias purpurea Spondias mombin | Forage, edible, timber | Stakes |
| | Huizache | Acacia farnesiana | Firewood, timber | Stakes |
| | Nopal | Nopalea dejecta | Edible | Shoots |
| | Cruceta | Acanthocereus tetragonus | Edible | Shoots |
| CF | Izote | Yucca gigantea | Edible, timber | Stakes |
| | Espino | Acacia pennatula | Firewood, timber | Stakes |
| | Gasparito | Erythrina americana | Edible, ornamental, firewood | Seedlings |
| | Liquidámbar | Liquidambar styraciflua | Timber, firewood, construction | Stakes, shoots, root shoots |
| | Sauco | Sambucus mexicana | Medicinal, ornamental | Stakes |
| POF | Maguey | Agave salmiana | Forage, medicinal, edible | Shoots of root |
| | Capulín | Prunus serotina | Timber, firewood, construction, edible, medicinal | Stakes, seedlings |
| | Tejocote | Crataegus gracilior | Medicinal, edible, firewood | Stakes, seedlings |
| | Aguacate | Persea americana | Edible | Seedlings |
| | Manzana | Malus domestica | Edible, firewood | Stakes, seedlings |
| | Ciruela | Prunus domestica | Edible | Stakes |
| | Ocote | Pinus patula | Timber, firewood, construction | Seeds (seedlings) |
| | Ciprés | Cupressus lusitanica | Timber, firewood, construction | Seeds (seedlings) |
| | Azumiate | Barkleyanthus salicifolius | Medicinal | Shoots |
| PF | Oyamel | Abies religiosa | Timber, construction | Seeds, seedlings, stakes |
| | Escobillo | Baccharis conferta | Firewood | Shoots |
| | Jarilla | Senecio cinerarioides | Medicinal, insecticide | Shoots |

Table 6. Usefulness and propagation method for plants in the live fences per ecosystem.

For the SS strata, we registered a moderate number of species (>40%) for medicinal use in the live fences of four ecosystems (TDF = 47%, CF = 48%, POF = 74%, and PF = 53%; $X^2 = 218, p < .05$, DF = 36). In the TDF ecosystem, we also documented that 25% of the vegetation was comprised of edible plants. Other uses revealed values between 14% and 1%, including timber, industrial, artisanal, fodder, and construction materials.

In general, 92% of the CT species in the live fences associated with all five ecosystems were useful plants. On the other hand, for the SS plants, we found that only 75% of the plants were useful ($X^2 = 71$, p < .05, DF = 4).

Management and Use of Live Fences

In the case of the TEF ecosystem, the most important land use was for cattle ranching whereas in the PF areas the land is used for the husbandry of goats and sheep. Regarding agricultural activities, we detected a high variation in the use of the land parcels (Figure 5). For example, in the TDF, different types of crops are managed (corn, coffee, sugar cane, chayote, and mango), whereas in CF and POF ecosystems, the land is mainly destined to produce corn for human and animal consumption.

According to the interviews that we carried out among the peasants, maintenance activities such as pruning and/or

weeding along the live fences is dependent on the use destined by each owner. The tools used for management purposes are primarily machetes and hoes. In particular, the pruning of the vegetation is biannual in TEF, TDF, and CF, meanwhile in the POF and PF, pruning is annual. Weeding takes place every 4–5 months, particularly in the tropical areas (TEF and TDF) and the moist humid areas (CF) where the growth of herbs and weeds is rapid. In some cases, all herbaceous plants are removed but in others, some of the important multipurpose useful species may be left. No fertilizer is used except in the POF ecosystem.

In general, the planting method to establish the live fences was by cutting thick branches at the beginning of the rainy season of specific tree species to form the fence posts. The peasants select branches about 2 m long and 15 cm thick and then these posts are placed in holes dug approximately 30 cm deep in the ground. In the case of the seedling plantations (e.g. *Pinus* spp. and *Cupressus* sp.), these were obtained from government and other non-government programs.

Discussion

As highlighted in the results, a total of 253 species were found in all the live fences sampled, which corresponded to 74 families and 181 genera of plants within the 150 transects



Figure 5. Some representative views of live fences in five contrasting ecosystems: A) Tropical evergreen forest (TEF), B) tropical deciduous forest (TDF), cloud forest (CF), C) pine–oak forest (POF), and D) pine forest (PF).

sampled (1.5 ha). The most represented families were Fabaceae, Asteraceae, and Euphorbiaceae. This number contrasts with that reported by Avendaño-Reyes and Acosta-Rosado (Avendaño Reves & Acosta Rosado, 2000) who identified 218 species in fences of 12 different habitats in another part of the state of Veracruz. It should be noted that in that study the CT category established within the fence line was registered and not the accompanying flora, whereas in the present study SS plants were taken into consideration which increased the number of species recorded. In addition, this study provides information on tolerated species by the owners (plants that are recruited from the reference vegetation that are not eliminated as they are considered as useful; cf. Table 6) (Wiersum, 1997) in these systems and the information provided contributes to the baseline of knowledge of biodiversity and management of the live fences (Stanturf et al., 2014).

Abiotic variables related to elevation (such as temperature, precipitation, and productivity) have a direct influence on species diversity in Neotropics (Rahbek, 1995). Especially in our study area, it has been shown that there is a different effect

of this variable on different plant groups (Bautista-Bello et al., 2019; Monge-González et al., 2020). Mainly, this pattern could be explained by the interactive effect of temperature and water availability known as the water-energy dynamics hypothesis (O'Brien, 1998). To our knowledge, this is the first study to analyze the effect of elevation on the diversity of live fences. However, other studies have shown that the use of live fences could improve the elevational migration to protect the resplendent quetzal (*Pharomacrus moccinno*) in Costa Rica (Powell & Bjork, 1994). The effectiveness of live fences in elevational gradients to promote the movement and dispersal of seeds by birds has been also found in Los Tuxtlas, Mexico (Estrada & Coates-Estrada, 2005).

The information obtained in this study broadens the knowledge of vegetation management in disturbed sites. Regardless of the anthropic activities, the establishment of perennials in live fences was of great importance in providing multiple ecological benefits (Pezo & Ibrahim, 2006), although these may only define the delimitation of land parcels. The high species richness of trees and shrubs found in the live fence system offers a variety of food resources (flowers and

fruits), host plants, resting sites, shelter, or perching sites (Bennett, 1990; Daily & Ehrlich, 1996; Guevara et al., 1998; Guevara & Laborde, 1993; Johnson & Beck, 1988; Siles et al., 2013) for the local fauna: For example, in the case of the tree species (*Alnus* spp. and *Pinus* spp.) which are found in POF and PF and form significant windbreak barriers for wildlife conservation mainly for birds (Medina et al., 2008), mammals (Burel, 1996), and butterflies (Tobar & Ibrahim, 2010). These species apart from being useful elements for the peasants also maintain ecological processes relevant to the preservation of many organisms (Chazdon et al., 2009), and the high proportion of useful species at all sites gives clear indications of a strong active species selection.

The species best represented in the live fence system belongs to the Fabaceae family, for example, in some cases *Leucaena leucocephala* was found along with corn crops, and this association may help increase soil fertility, as well leaf litter production (Tamayo-Chim & Orellana, 2007). The presence of legume species in these systems is important to aid in the development of nitrogen-rich soils (Budowski & Russo, 1993). In general, we also noted a high number of species belonging to the Asteraceae family in the fences adjacent to agricultural activities, which regardless of being under management and close to native vegetation sites facilitated the invasion of weeds (Radosevich et al., 2007). Also, the species belonging to this family can offer several resources important for pollinators (i.e., bees, bumblebees, and butterflies).

It was evident in some fences, there were trees surrounded by mature forest, therefore, the main dispersal vectors are animals that carry propagules from the forest edge and the live fence functions as a germination site, where important seeds may be stored in the soil, and later triggered for establishment (Ruiz-Guerra et al., 2014). Overall, live fences can be considered potentially functional because, in addition to being part of the anthropogenic landscape, they act as reservoirs of diversity, where ecological processes favorable to the conservation of organisms occur (Gliessman et al., 1998). Previous studies have also confirmed that live fences have the potential to increase landscape connectivity (Estrada & Coates-Estrada, 2001; Harvey et al., 2003). In addition, fences constitute conservation elements by functioning as reservoirs of native species (Dirzo et al., 2009), as was documented in our all-sampling sites, which captured germplasm from patches of adjacent forests (Avendaño Reyes & Acosta Rosado, 2000; Harvey et al., 2008).

Our data show differentiation in richness: the most diverse fences were those adjacent to TEF and TDF (10–500 m.a.s.l), and the smallest in POF and PF (2000 and 3500 m.a.s.l). At low altitudes there is a high heterogeneity of established flora, however, in the higher altitudes, the diversity of species of related ecosystems is restricted. These are sites with less arboreal diversity, and locally "dead" wood fences are used as these require less maintenance. In terms of true diversity, the highest value stands out in the

fences associated with the CF (q1 and q2), which present a greater uniformity in distribution and the establishment of the number of individuals in each species. Here also are the living fences where the largest number of botanical families was recorded, which makes these especially important in terms of conservation because this ecosystem is highly threatened, and the use of living fences is being replaced by prefabricated poles.

The differences in the composition of the live fences among ecosystems and productive areas were evident since they are dependent on the ecological and physical conditions, as well as the methods used by peasants to establish and manage the fences (Harvey et al., 2003, 2005). The greater use of various plant species occurs in four ecosystems (TEF, TDF, CF, and POF), where the highest biological heterogeneity is concentrated, while at higher elevations (PF) where there is less tree diversity, peasants choose to use dead wood, stone, and concrete posts for fences. As mentioned beforehand, the number of individuals or development of plant species in the live fences will depend on the history of land use (pastures or crops), species availability, resource demand, parcel size (Ibrahim et al., 2007), and management, which will either decrease or increase diversity (Huston, 2004).

In fences adjacent to the TEF, we found a low similarity and overlap between strata, due to the fact that plants in recruitment typical of mature forest were recorded, such as Brosimum alicastrum, Amphitecna tuxtlensis, Mortoniodendron guatemalense, and Nectandra ambigens. An important finding in the fences associated with TEF was the "capture" of cacti such as: Neobuxbaumia euphorbioides, N. scoparia, Nopalea dejecta, and Pilosocereus leucocephalus, which explains the high heterogeneity of species and low similarity values. Psychotria erythrocarpa, a typical arboreal species of mature forests, was also reported by Guevara et al. (1998). In the fences associated with CL, they are capable of retaining species that are found in other elements of the landscape, for example, *Piper hispidum*, a typical shrub of more conserved areas and Smilax moranensis, a liana commonly used for the production of sarsaparilla. A greater similarity in species composition was found in the fences adjacent to the POF and PF (Morisita = 0.71); In the first one, Sambucus mexicana stands out in regeneration vegetation, while in PF, there is Ribes microphyllum, both are used for medicinal purposes.

The species that we registered in the fences are managed by locals who have lived most of their lives in each of the communities studied; therefore, the value that the live fences represent will depend on the location of the land parcel and its use and will also be conditioned to the traditional knowledge of the flora of each community. For example, *Bursera simaruba* in this study proved to be a dominant tree in the establishment of live fences in the TEF and TDF ecosystems. It is a species that is tolerant to water stress and easily reproduced using branch posts, characteristics which may be important to determine its degree of use by peasants (Siles et al., 2013).

The highest percentage of useful flora was found for CT species that form the live fences. This was supported by data from the ecosystems such as the TDF and CF, where the species represent important resources that can be used according to the needs of the local inhabitants (Wiersum, 1997). In addition, the presence of some tolerated plants in the shrubs and saplings category is also advantageous as they may provide other services when they reach the CT state. The data also showed that native plants (Pulido-Santacruz & Renjifo, 2011) and even exotic plants are tolerated in fences, although not planted directly, but are maintained for their aesthetic or edible value (Calle et al., 2017).

The plants established in the surveyed live fences have several uses, such as medicinal, edible, ornamental, fuel, timber, industrial, artisanal, fodder, and construction materials. We did not find any reports on the use of some of the species. Most of the species recorded were related to different categories of uses such as medicinal, edible, fence posts, construction materials, firewood, shade, ornamental, and fodder (Stanturf et al., 2014). The use of these species in the live fences may reduce the pressure on the forested areas by limiting the extraction or felling of native trees. The peasants of the properties confirmed that the products obtained from the live fences are sold in the local markets, thus confirming that a system of this nature becomes ecologically and economically more viable. The establishment of live fences guarantees peasants economic savings in the future, in addition to providing an added ecological value to their land, this way of managing the agroforestry landscape is consistent with work carried out in other culturally contrasting regions in Mexico (Rendón-Sandoval et al., 2020).

Finally, our data provide a distinguishable pattern: the configuration of live fences is structured by three processes: the selection of the initial trees based on the use of adjacent land, the viability of the arrival of zoochorous species, and the tolerance management of the owners for species that are established in the fences according to their immediate utility, which is highly associated with local flora. This aspect is of utmost significance for biodiversity conservation of the flora from the conserved reference ecosystems, and the importance of these live fences is much more beyond being mistakenly considered as simple division lines among land parcels.

We suggest that peasants should receive technical training and information relevant to the methods to diversify their live fences to include several different species. The diversification of tree species would increase the productivity of these live fence systems in terms of goods and services obtained, along with the important contribution to the conservation of biodiversity, protection against soil erosion, conservation of water resources, and soil nutrients (Arroyo-Rodríguez et al., 2020). The advantages of using live fences should be recognized and managed correctly so that they are not replaced in the future by wooden or concrete fence posts. Therefore, it is necessary to understand and exchange technical experiences regarding the management practices traditionally carried out by the peasants, to expand the range of use of present or potential plant resources in the live fences within different ecosystems.

Meanwhile, the greater the extent, structural complexity and diversity of species that are used in live fences will contribute to the preservation of local biodiversity and their increased economic value. The peasants may consider the species used in the live fences and the associated vegetation, as integral elements of the productive system. The floristic inventory obtained in this research can serve as a guide to understand and promote multiple-use species in live fences. Although in this study the techniques reported on the management of species under the live fence systems are limited; their application should be carried out properly. We also suggest that priority should be given to the use of native species, and excessive pruning should be controlled and avoided during the dry season. This will ensure species richness and impact contribute to the conservation of biodiversity according to the type of vegetation in each ecosystem. It is especially necessary to promote the use of live fences in the CF due to its high representation of species and its high level of threat about conservation status. On the other hand, to determine the commercial viability of the live fences, it is necessary to carry out a study on the economic value of both the products generated, as well as the profits obtained from their sale in the local markets.

Appendix A

List of species present in the live fences in the five ecosystems under study. The different ecosystem types in which the species were registered is indicated (TEF = tropical evergreen rainforest, TDF = tropical de forest, CF = cloud forest, POF = pine–oak forest, and PF = pine forest). *The asterisks indicate introduced plant species per ecosystem type.

| Family/species | TEF | TDF | CF | POF | PF |
|---|-----|-----|----|-----|----|
| - Achatocarpaceae | | | | | |
| Achatocarpus nigricans Triana | | Х | | | |
| Adoxaceae | | | | | |
| Sambucus mexicana C. Presl ex DC. | | | Х | Х | |
| Agavaceae | | | | | |
| Agave salmiana Otto ex Salm-Dyck | | | | Х | Х |
| Anacardiaceae | | | | | |
| Comocladia macrophylla (Hook. and Arn.) L. Riley | | Х | | | |
| Mangifera indica L. | X* | X* | | | |
| Rhus terebinthifolia Schltdl. and Cham. | | Х | | | |
| Spondias mombin L. | | Х | | | |
| Spondias purpurea L. | Х | Х | | | |
| Spondias radlkoferi Donn. Sm. | Х | | | | |
| Annonaceae | | | | | |
| Annona cherimola Mill. | | Х | Х | | |
| Annona muricata L. | | Х | | | |
| Rollinia mucosa (Jacq.) Baill. | X* | | | | |
| Apocynaceae | | | | | |
| Cascabela thevetioides (Kunth) Lippold | | Х | | | |
| Gonolobus sp. | | Х | | | |
| Plumeria rubra L. | Х | х | | | |
| Tabernaemontana alba Mill. | X | | | | |
| Tabernaemontana donnell-smithii Rose | Х | | | | |
| Araliaceae | | | | | |
| Oreopanax xalapensis (Kunth) Decne. and Planch. | | | Х | | |
| Arecaceae | | | | | |
| Attalea butyracea (Mutis ex L. f.) Wess. Boer | Х | | | | |
| Asparagaceae | | | | | |
| Yucca gigantea Lem. | | х | Х | х | |
| Asteraceae | | | | | |
| Baccharis conferta Kunth | | | | Х | Х |
| Barkleyanthus k (Kunth) H. Rob. and Brettell | | | | X | X |
| Brenandendron donianum (DC.) H. Rob. | | х | | | |
| Calea urticifolia (Mill.) DC. | | X | | | |
| Calea zacatechichi Schltdl. | | | Х | | |
| Cirsium jorullense (Kunth) Spreng. | | | | Х | |
| Eupatorium sp. | х | х | | | |
| Montanoa sp. | | x | | | |
| Roldana barba-johannis (DC.) H. Rob. and Brettell | | | | | х |
| Senecio angulifolius DC. | | | | | X |
| Senecio cinerarioides Kunth | | | | | X |
| Stevia monardifolia Kunth | | | | | X |
| Symphoricarpos microphyllus Kunth | | | | | X |
| Trixis inula Crantz | | х | | | ~ |
| Verbesina sp. | | X | | | |
| Vernonanthura deppeana (Less.) H. Rob. | | X | | | |
| Vernonia sp. | | X | | | |

⁽continued)

| Family/species | TEF | TDF | CF | POF | PF |
|---|-----|-----|----|-----|----|
| Vernonia sp. l | | | х | | |
| Betulaceae | | | | | |
| Alnus jorullensis Kunth. | | | | | Х |
| Carpinus caroliniana Walter. | | | Х | | |
| Bignoniaceae | | | | | |
| Amphitecna tuxtlensis A.H. Gentry | Х | | | | |
| Crescentia cujete L. | Х | | | | |
| Handroanthus chrysanthus (Jacq.) S.O. Grose | | Х | | | |
| Tecoma stans (L.) Juss. Ex Kunth | | Х | | | |
| Boraginaceae | | | | | |
| Cordia alliodora (Ruiz and Pav.) Oken | Х | Х | | | |
| Cordia spinescens L. | Х | | | | |
| Tournefortia glabra L. | | | Х | | |
| Burseraceae | | | | | |
| Bursera simaruba (L.) Sarg. | Х | Х | Х | | |
| Cactaceae | | | | | |
| Acanthocereus tetragonus (L.) Hummelinck | | Х | | | |
| Neobuxbaumia euphorbioides Buxb. | | Х | | | |
| Neobuxbaumia scoparia (Polselg.) Backeb. | | Х | | | |
| Nopalea dejecta (Salm-Dyck) Salm-Dyck | | Х | Х | | |
| Pilosocereus leucocephalus (Poselger) Byles and G.D. Rowley | Х | | | | |
| Cannabaceae | | | | | |
| Celtis caudata Planch. | | Х | | | |
| Trema micrantha (L.) Blume | | | Х | | |
| Capparaceae | | | | | |
| Quadrella incana (Kunth) Iltis and Cornejo | | Х | | | |
| Caprifoliaceae | | | | | |
| Lonicera japonica Thunb. | | | | X* | |
| Celastraceae | | | | | |
| Salacia cordata (Miers) Mennega | Х | | | | |
| Pristimera celastroides (Kunth) A.C.Sm. | | X | | | |
| Chloranthaceae | | | | | |
| Hedyosmum mexicanum C. Cordem. | | | Х | | |
| Chrysobalanaceae | | | | | |
| Hirtella racemosa Lam. | Х | | | | |
| Clethraceae | | | | | |
| Clethra mexicana DC. | | | Х | | |
| Clusiaceae | | | | | |
| Garcinia intermedia (Pittier) Hammel | Х | | | | |
| Cupressaceae | | | | | |
| Cupressus Iusitanica Mill. | | Х | Х | Х | Х |
| Ebenaceae | | | | | |
| Diospyros acapulcensis Kunth | | Х | | | |
| Ericaceae | | | | | |
| Arbutus xalapensis Kunth | | | | | Х |
| Erythroxylaceae | | | | | |
| Erythroxylum havanense Jacq. | | Х | | | |
| Euphorbiaceae | | | | | |
| Adelia barbinervis Cham. and Schltdl. | | Х | | | |
| Alchornea latifolia Sw. | | X | Х | | |
| Cnidoscolus aconitifolius (Mill.) I.M. Johnst. | | Х | | | |
| Croton ciliatoglandulifer Ortega | | Х | | | |

(continued)

(continued)

| Family/species | TEF | TDF | CF | POF | PF |
|--|-----|--------|----|-----|----|
| Croton micans Sw. | | Х | | | |
| Croton schiedeanus Schltdl. | Х | | | | |
| Croton glabellus L. | | Х | | | |
| Euphorbia pteroneura A. Berger | | Х | | | |
| Jatropha curcas L. | Х | | | | |
| Omphalea oleifera Hemsl. | Х | | | | |
| Sapium lateriflorum Hemsl. | Х | | | | |
| Fabaceae | | | | | |
| Acacia angustissima (Mill.) Kuntze | | Х | | | |
| Acacia farnesiana (L.) Willd. | | х | | | |
| Acacia macracantha Willd. | | х | | | |
| Acacia pennatula (Schltdl. and Cham.) Benth. | | х | Х | | |
| Acosmium panamense (Benth.) Yakovlev | Х | | | | |
| Calliandra houstoniana (Mill.) Standl. | | х | | | |
| Desmodium sp. | | х | | | |
| Dialium guianense (Aubl.) Sandwith | х | | | | |
| Diphysa americana (Mill.) M. Sousa | | Х | | | |
| Erythrina americana Mill. | | X | Х | | |
| Erythrina folkersii Krukoff and Moldenke | х | | | | |
| Eysenhardtia polystachya (Ortega) Sarg. | ~ | Х | | | |
| Gliricidia sepium (Jacq.) Walp. | х | X | | | |
| Indigofera sp. | Х | X | | | |
| Inga jinicuil Schltdl. | | X | х | | |
| Leucaena diversifolia (Schltdl.) Benth. | | Х | Λ | | |
| Leucaena leucocephala (Lam.) de Wit. | | X | х | | |
| Lonchocarpus guatemalensis Benth. | х | | ~ | | |
| Lonchocarpus sericeus (Poir.) DC. | X | | | | |
| Lonchocarpus sp. | ^ | Х | | | |
| Lysiloma microphylla Benth | | x | | | |
| | | × | | | |
| Senna atomaria (L.) H. S. Irwin and Barneby | х | ~ | | | |
| Senna multijuga (Rich.) H.S. Irwin and Barneby | ~ | × | | | |
| Senna pallida (Vahl) H. S. Irwin and Barneby | х | X X | | | |
| Vachellia cornigera (L.) Seigler and Ebinger | X | ~ | | | |
| Fagaceae | | | × | | |
| Quercus affinis M. Martens and Galeotti | | | Х | X | |
| Quercus laurina Raf. | | | X | Х | |
| Quercus leiophylla A. DC. | | | X | | |
| Quercus xalapensis Bonpl. | | | Х | | |
| Ruprechtia fusca Fernald | | Х | | | |
| Gesneriaceae | | | | | |
| Moussonia deppeana (Schltdl. and Cham.) Hanst. | | | Х | | |
| Grossulariaceae | | | | | |
| Grossularia microphylla (Kunth) Coville and Britton | | | | | |
| Ribes affine Kunth | | | | | |
| Ribes ciliatum Humb. and Bonpl. ex Roem. and Schult. | | | | | |
| Ribes microphyllum Kunth. | | | | | |
| Hamamelidaceae | | | | | |
| Liquidambar styraciflua L. | | | Х | | |
| Hernandiaceae | | | | | |
| Gyrocarpus jatrophifolius Domin | | х | | | |
| Juglandaceae | | | | | |
| Juglans olanchana Standl. and L.O. Williams | | | Х | | |

⁽continued)

| Family/species | TEF | TDF | CF | POF | PF |
|---|-----|------------|----|-----|----|
| Lamiaceae | | | | | |
| Clerodendrum bungei Steud. | | | Х | | |
| Lauraceae | | | | | |
| Nectandra ambigens (S.F. Blake) C.K. Allen | Х | | | | |
| Nectandra salicifolia (Kunth) Nees | Х | | | | |
| Ocotea dendrodaphne Mez | Х | | | | |
| Persea americana Mill. | Х | | Х | | |
| Persea schiedeana Nees | Х | | | | |
| Malpighiaceae | | | | | |
| Bunchosia sp. | | Х | | | |
| Gaudichaudia albida Schltdl. and Cham. | | Х | | | |
| Heteropterys brachiata (L.) Kunth | | Х | | | |
| Malvaceae | | | | | |
| Abutilon trisulcatum (Jacq.) Urb. | | Х | | | |
| Ceiba aesculifolia (Kunth) Britten and Baker f. | | X | | | |
| Guazuma ulmifolia Pers. | | X | | | |
| Hampea nutricia Fryxell | х | | | | |
| Heliocarpus appendiculatus Turcz. | | | х | | |
| Heliocarpus pallidus Rose | | Х | | | |
| Malvaviscus arboreus Cav. | х | X | х | | |
| Mortoniodendron guatemalense Standl. and Steyerm. | X | X | X | | |
| Pachira aquatica Aubl. | X | | | | |
| Phymosia rosea (DC.) Kearney | X | | | | |
| Pseudobombax ellipticum (Kunth) Dugand | X | Х | | | |
| Melastomataceae | A | Λ | | | |
| Conostegia arborea Steud. | | | х | | |
| Conostegia xalapensis (Bonpl.) D. Don ex DC. | х | | ~ | | |
| | X | | | | |
| Miconia argentea (Sw.) DC. Miconia glaberrima (Schtdl.) Naudin | ~ | | х | | |
| Meliaceae | | | ~ | | |
| Cedrela odorata L. | х | х | | | |
| Guarea glabra Vahl | X | ~ | | | |
| Swietenia humilis Zucc. | ~ | х | | | |
| | х | × | х | | |
| Trichilia havanensis Jacq. Trichilia hirta L. | ^ | × | ^ | | |
| Trichilia martiana C. DC. | V | ^ | | | |
| | Х | | | | |
| Moraceae | | V * | | | |
| Artocarpus heterophyllus Lam. | X | X* | | | |
| Brosimum alicastrum Sw. | X | Х | | | |
| Ficus americana Aubl. | X | | | | |
| Ficus aurea Nutt. | X | X | Х | | |
| Ficus cotinifolia Kunth | X | Х | | | |
| Ficus obtusifolia Kunth | Х | | | | |
| Ficus pertusa L.f. | | Х | | | |
| Poulsenia armata (Miq.) Standl. | Х | | | | |
| Myricaceae | | | | | |
| Morella cerifera (L.) Small | | | Х | | |
| Myrsinaceae | | | | | |
| Myrsine coriacea (Sw.) R.Br. ex Roem. and Schult. | | | Х | | |
| Myrtaceae | | | | | |
| Eugenia acapulcensis Steud. | Х | | | | |
| Eugenia capuli (Schltdl. and Cham.) Hook. and Arn. | Х | | | | |

(continued)

| Family/species | TEF | TDF | CF | POF | PF |
|---|-----|-----|----|-----|----|
| Eugenia macrocarpa Schltdl. and Cham. | х | | | | |
| Eugenia nigrita Lundell | Х | | | | |
| Psidium guajava L. | Х | Х | х | | |
| Nyctaginaceae | | | | | |
| Bougainvillea glabra Choisy | | | х | | |
| Pisonia aculeata L. | | Х | | | |
| Oleaceae | | | | | |
| Fraxinus dubia (Willd. Ex Schult. and Schult. F.) P.S. Green and M. Nee | | Х | | | |
| Ligustrum lucidum W. T. Aiton | | | X* | | |
| Ximenia americana L. | | х | | | |
| Papaveraceae | | | | | |
| Bocconia frutescens L. | | х | Х | | |
| Passifloraceae | | | | | |
| Passiflora foetida L. | | Х | | | |
| Passiflora sp. | | X | | | |
| Picramniaceae | | | | | |
| Picramnia antidesma Sw. | | | х | | |
| Pinaceae | | | ~ | | |
| Abies religiosa (Kunth) Schtdl. and Cham. | | | | | х |
| Pinus ayacahuite Ehrenb. ex Schltdl. | | | | Х | X |
| | | | х | × | ^ |
| Pinus patula Schltdl. and Cham. | | | ~ | ~ | v |
| Pinus pseudostrobus Lindl. | | | | | Х |
| Piperaceae | X | | | | |
| Piper amalago L. | Х | | X | | |
| Piper arboreum Aubl. | | | X | | |
| Piper auritum Kunth | X | | X | | |
| Piper hispidum Sw. | X | | Х | | |
| Piper sp. | X | | | | |
| Piper umbellatum L. | X* | | | | |
| Plantaginaceae | | | | | |
| Penstemon gentianoides (Kunth) Poir. | | | | | Х |
| Platanaceae | | | | | |
| Platanus mexicana Moric. | | | Х | | |
| Poaceae | | | | | |
| Chusquea sp. | | | Х | | |
| Olyra latifolia L. | | Х | | | |
| Polygalaceae | | | | | |
| Monnina xalapensis Kunth | | | | Х | |
| Antigonon leptopus Hook. and Arn. | | Х | | | |
| Coccoloba barbadensis Jacq. | Х | | | | |
| Coccoloba montana Standl. | Х | | | | |
| Primulaceae | | | | | |
| Ardisia compressa Kunth | Х | | Х | | |
| Ranunculaceae | | | | | |
| Clematis dioica L. | | Х | | | |
| Colubrina triflora Brongn. ex Sweet | | Х | | | |
| Frangula discolor (Donn. Sm.) Grubov | | | Х | | |
| Rhamnus humboldtiana Will. ex Schult. | | Х | | | |
| Rhamnus pompana M.C. Johnst. and L.A. Johnst. | | | Х | | |
| Ziziphus amole (Sessé and Moc.) M.C. Johnst. | | х | | | |
| Osaceae | | | | | |
| otoneaster þannosus Franch. | | | | | |

(continued)

| Family/species | TEF | TDF | CF | POF | PF |
|--|-----|-----|----|-----|----|
| Crataegus gracilior J.B.Phipps | | | | | |
| Crataegus sp. | | | | Х | |
| Eriobotrya japonica (Thunb.)Lindl. | | | X* | | |
| alus domestica Borkh. | | | | | |
| Prunus domestica L. | | | | | |
| Prunus serotina Ehrh. | | | | Х | |
| Rubus adenotrichus Schltdl. | | | Х | | |
| Rubiaceae | | | | | |
| Coffea arabica L. | | X* | X* | | |
| Hoffmannia excelsa (Kunth) K. Schum. | | | Х | | |
| Palicourea tetragona (Donn. Sm.) C.M. Taylor | Х | | | | |
| Psychotria erythrocarpa Schltdl. | | Х | | | |
| Psychotria limonensis K. Krause | Х | | | | |
| , Randia aculeata L. | | | Х | | |
| Randia armata (Sw.) DC. | Х | | | | |
| Rutaceae | | | | | |
| Citrus limon (L.) Osbeck | | | X* | | |
| Citrus sinensis (L.) Osbeck | X* | | | | |
| Zanthoxylum caribaeum Lam. | | Х | | | |
| Zanthoxylum fagara (L.) Sarg. | | x | | | |
| Zanthoxylum melanostictum Schltdl. and Cham. | | | х | | |
| Zanthoxylum riedelianum Engl. | х | | ~ | | |
| Zanthoxylum sp. | X | | х | | |
| Salicaceae | | | Λ | | |
| Casearia corymbosa Kunth | х | х | | | |
| Casearia sp. | Х | X | | | |
| Pleuranthodendron lindenii (Turcz.) Sleumer | х | ~ | | | |
| Populus mexicana Wesm.Ex DC. | ~ | х | | | |
| Prockia crucis P. Browne ex L. | | x | | | |
| | | ^ | V | | |
| Xylosma flexuosa (Kunth) Hemsl. Secimente | | | Х | | |
| Sapindaceae | | X | | | |
| Cardiospermum grandiflorum Sw. | V | Х | | | |
| Cupania dentata Moc. and Sessé ex DC. | X | | | | |
| Cupania glabra Sw. | X | | | | |
| Paullinia clavigera Schltdl. | Х | | | | |
| Paullinia tomentosa Jacq. | | Х | | | |
| Serjania caracasana (Jacq.) Willd. | | Х | | | |
| Serjania triquetra Radlk. | | Х | | | |
| Sapotaceae | | | | | |
| Sideroxylon sp. | Х | | | | |
| Schoepfiaceae | | | | | |
| Schoepfia schreberi J.F. Gmel. | | х | | | |
| Scrophulariaceae | | | | | |
| Buddleja parviflora Kunth | | | | х | |
| Smilacaceae | | | | | |
| Smilax moranensis M. Martens and Galeotti | | | Х | | |
| Solanaceae | | | | | |
| Brugmansia arborea (L.) Steud. | Х | | | | |
| Brugmansia candida Pers. | | | Х | | |
| Capsicum annuum L. | Х | | | | |
| Cestrum dumetorum Schltdl. | | Х | | | |
| estrum nocturnum L. | | Х | Х | | |

(continued)

(continued)

| Family/species | TEF | TDF | CF | POF | PF |
|---|-----|-----|----|-----|----|
| Cestrum sp. | | Х | | | |
| Cestrum tomentosum L.f. | | Х | Х | | |
| Lycianthes lenta (Cav.) Bitter | | Х | | | |
| Solanum diphyllum L. | | | Х | | |
| Solanum ferrugineum Jacq. | | | Х | | |
| Solanum lanceolatum Cav. | | | Х | | |
| olanum torvum Sw. | | | Х | | |
| Urticaceae | | | | | |
| Myriocarpa longipes Liebm. | Х | | | | |
| Verbenaceae | | | | | |
| Citharexylum mocinoi D. Don | | | Х | | |
| Lippia myriocephala Schltdl. and Cham. | | | Х | | |
| Violaceae | | | | | |
| Orthion veracruzense Lundell | Х | | | | |
| Vitaceae | | | | | |
| Cissus verticillata (L.) Nicolson and C.E. Jarvis | | Х | | | |
| Vitis tiliifolia Humb. and Bonpl. Ex Schult. | | | х | | |
| Vochysiaceae | | | | | |
| Vochysia guatemalensis Donn. Sm. | Х | | | | |

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ORCID iDs

Jorge Antonio Gómez Díaz b https://orcid.org/0000-0001-8182-7584 Juan Carlos Lopez-Acosta b https://orcid.org/0000-0002-3817-9099

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