

# 2

---

## *Tropical Dry Forest Ecological Succession in Mexico: Synthesis of a Long-Term Study*

---

Mauricio Quesada, Mariana Álvarez-Añorve, Luis Ávila-Cabadilla, Alicia Castillo, Martha Lopezaraiza-Mikel, Silvana Martén-Rodríguez, Victor Rosas-Guerrero, Roberto Sáyago, Gumersindo Sánchez-Montoya, José Miguel Contreras-Sánchez, Francisco Balvino-Olvera, Sergio Ricardo Olvera-García, Sergio Lopez-Valencia, and Natalia Valdespino-Vázquez

### CONTENTS

2.1	Introduction.....	17
2.2	Ecosystem Structure and Composition .....	19
2.2.1	Species Richness .....	20
2.2.2	Species Density .....	21
2.2.3	Species Composition .....	21
2.2.4	Vegetation Structure.....	24
2.3	Phenology .....	27
2.3.1	Leafing.....	27
2.3.2	Flowering and Fruiting.....	27
2.4	Successional Changes in Vertebrate Communities.....	28
2.4.1	Birds.....	28
2.4.2	Bats.....	28
2.5	Human Dimensions .....	29
2.6	Conclusions and Recommendations.....	30

---

### 2.1 Introduction

The current status and rates of conversion of mature tropical forests indicate that these habitats will eventually disappear, leaving behind a complex landscape matrix of agricultural fields and forest patches under different levels of succession. Tropical dry forests (TDFs) are not an exception, and the current management derived from human activities will clearly result in the complete loss of this habitat worldwide (Quesada and Stoner 2004; Miles et al. 2006; Quesada et al. 2009). The TDFs have been extensively transformed and occupied by urban and agricultural areas at significantly higher rates than

tropical rainforests (Murphy and Lugo 1986a). Therefore, understanding tropical succession in the context of ecological and human dimensions represents one of the major challenges to promoting and developing conservation and management programs for this threatened ecosystem.

Few studies have analyzed ecological succession in TDFs, indicating contrasting results; in some cases, a relatively faster structural recovery is found for this system than for other tropical systems (i.e., Ceccon et al. 2002; Ruiz et al. 2005; Vieira and Scariot 2006), but in others, a slower process is found in TDFs than in wet forests in terms of plant growth and other developmental features (Ewel 1977; Murphy and Lugo 1986a). However, the interpretation of succession is not clear because the recovery of species richness and the composition are dependent on structural change (Sheil 2001; Ceccon et al. 2002; Pascarella et al. 2004; Ruiz et al. 2005; Toledo and Salick 2006; Quesada et al. 2009; Alvarez-Añorve et al. 2012). In addition, some studies claim that TDFs are relatively simple and small in structure and composition, and that they recover predominantly through coppicing after disturbance (Ewel 1977; Murphy and Lugo 1986a; Chazdon et al. 2007). However, Quesada et al. (2009, 2011) challenge this view, as the predominant mode of reproduction in TDFs is through a wide variety of sexual systems in which seeds are mainly produced via outcrossing. If coppicing or asexual reproduction were the main drivers of regeneration, changes in species composition along secondary succession would not be expected. Several studies that analyze a chronosequence have found differences in species composition in TDFs. Therefore, the regeneration of TDFs is expected to be slow and very susceptible to human disturbance because the growth rate of many tree species is slow, reproduction is highly seasonal, and most plants are mainly outcrossed and dependent on animal pollination (Bawa 1974, 1990; Frankie 1974; Murphy and Lugo 1986a; Hamrick and Murawski 1990; Bullock 1995; Jaimes and Ramirez 1999; Cascante et al. 2002; Fuchs et al. 2003; Quesada et al. 2001, 2004, 2009). Another important aspect to consider in the process of regeneration is the functional recovery of the community, which identifies groups of plants and animals that exhibit similar responses to environmental conditions and have similar effects on dominant ecosystem processes that are associated with successional stages (Gitay and Noble 1997; Lebrija-Trejos et al. 2010; Alvarez-Añorve et al. 2012; Avila-Cabadilla et al. 2012). Only a few studies have simultaneously evaluated TDF succession in floristic, structural, and functional terms.

Alvarez-Añorve et al. (2012) found that plant functional traits along succession change from those that maximize heat dissipation in early successional stages to those that enhance light acquisition and water use in late successional stages. This study suggests that the functional recovery of TDFs could take longer than inferred when the process is evaluated from just a floristic and/or structural perspective, but more studies from other tropical regions are required to corroborate patterns of functional succession. In addition, the variation in vertebrate guild assemblages is associated with the variation in landscape habitat attributes under different successional stages.

**TABLE 2.1**

Tropi-Dry Plot Abbreviations and Age of Abandonment in 2004 and 2009

Successional Stage	Plots	Age in 2004 (Years of Abandonment)	Age in 2009 (Years of Abandonment)
Initial (pastures)	P1-P3	0	5
Early	E1-E3	3–5	8–10
Intermediate	I1-I3	8–12	13–17
Late	L1-L3	>50	>55

Avila-Cabadilla et al. (2012) found that nectarivore bats tend to be associated with TDF patches, whereas frugivore bats are associated with riparian forests. This probably reflects the prevalence of species that produce nectar resources for bats in dry forests, and of species which produce fruits that are eaten and dispersed by bats in riparian forests. In conclusion, the main mechanisms of succession and regeneration of TDFs still remain unexplored, and more efforts are required to understand the ecological processes of these important ecosystems.

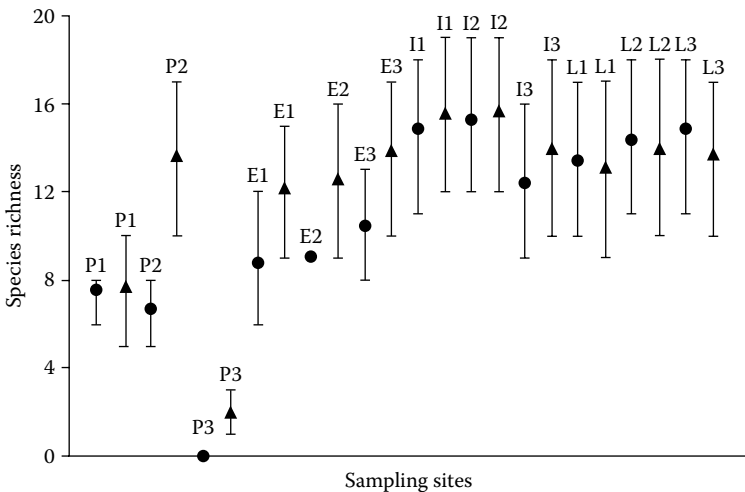
The main goal of this synthesis is to understand the successional process underlying the natural regeneration of TDFs for the development of conservation strategies in the Chamela–Cuixmala Biosphere Reserve region, which is located along the central Pacific coast of Mexico (Figure 1.2). Little is known about the regeneration process of these forests, and our study is one of the few that provides basic and applied ecological information on the succession in TDFs in Mexico. To characterize TDF successional patterns, we assessed the successional changes in vegetation attributes (i.e., structure, species composition), ecosystem functioning (i.e., functional traits, herbivory, phenology), and fauna diversity and abundance in a highly diverse Mexican TDF. For this purpose, we performed a five-year study in a chronosequence that represented four TDF successional stages: initial, early, intermediate, and late (Table 2.1). We also conducted socio-ecological research to understand the changes in land-use history and their effects on succession and forest regeneration of TDFs (see Chapter 21 for an in-depth comparative study). We emphasize the need to integrate ecological knowledge with the human dimension as a tool that supports sound conservation, management, and understanding of TDFs.

## 2.2 Ecosystem Structure and Composition

Between 2004 and 2009, vegetation structure and species composition of the plots were compared among the different successional stages. Changes in the chronosequence were compared within plots, between successional stages, and over the course of the five-year study (Table 2.1). The study design and methods are detailed in Chapter 1.

### 2.2.1 Species Richness

In general, species richness increased with successional age (Figure 2.1), and intermediate stage plots showed similar species richness than did late successional plots. This parameter differed significantly among successional stages during both years (Kruskal–Wallis  $\chi^2_{(2004)} = 9.46$ ,  $df = 3$ ,  $p = 0.024$ ;  $\chi^2_{(2009)} = 8.08$ ,  $df = 3$ ,  $p = 0.044$ ) (Figure 2.1). In 2004, pastures and early stages had a significantly lower species richness than intermediate and late stages. These results indicate that management practices used in the chronosequence plots left many species of late successional stages standing in the intermediate plots. In 2009, early, intermediate, and late successional stages were similar to each other; only pastures differed from all the other three successional stages. During the same, pastures (5 years old by 2009) also showed high intra-stage variations, suggesting higher stochasticity in early stages. The lowest species richness occurred at site P3, which is dominated by trees and shrubs of the genus *Mimosa* (Leguminosae) and that is surrounded by other pastures. In contrast, the highest species richness occurred at site P2, which is surrounded by secondary forests that could facilitate the regeneration of several species. In general, from 2004 to 2009, the highest increase in species richness occurred in pastures, whereas there was no significant change in intermediate and late successional plots. Plots that are 8 years old and older present similar species richness, indicating a relatively rapid regeneration and recovery. This suggests an important role



**FIGURE 2.1**

Species richness of Tropi-Dry plots under different successional stages for years 2004 (circles) and 2009 (triangles). Species richness was rarified at 23 individuals. P1-P3 = pastures, E1-E3 = early successional plots, I1-I3 = intermediate successional plots, and L1-L3 = late successional plots.

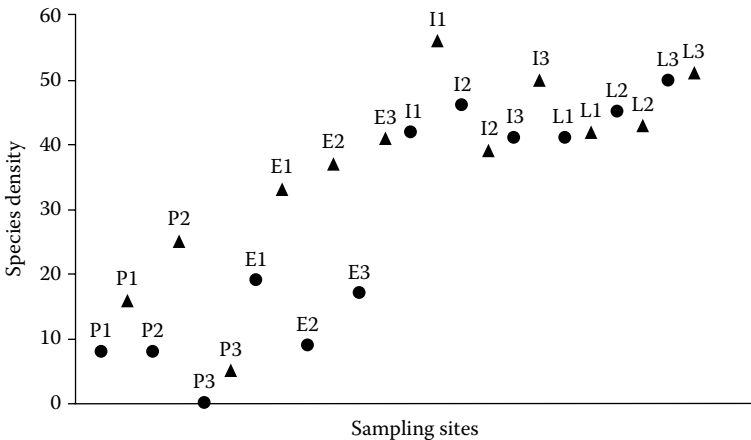
of the surrounding landscape attributes of the vegetation matrix in the successional process of this system.

### 2.2.2 Species Density

Species density differed significantly among successional stages and increased with successional age (ANOVA 2004  $F_{(3,8)} = 19.4$ ,  $p = 0.0004$ ; ANOVA 2009  $F_{(3,8)} = 12.4$ ,  $p = 0.002$ ) (Figure 2.2). In 2004, similar to species richness, pastures and early stages were significantly different from intermediate and late stages. In 2009, only pastures differed from other successional stages. The density parameter appears to be useful in differentiating successional stages as well as in predicting temporal dynamics from the chronosequence due to the following reasons: (1) Density showed a gradual increase along succession. (2) There were significant differences among successional stages. (3) Early successional plots of the year 2009 (8–10 years old) showed similar values to intermediate successional plots of the year 2004 (8–12 years old). (4) Pastures of the year 2009 (5 years old) showed similar values to early successional plots of the year 2004 (3–5 years old).

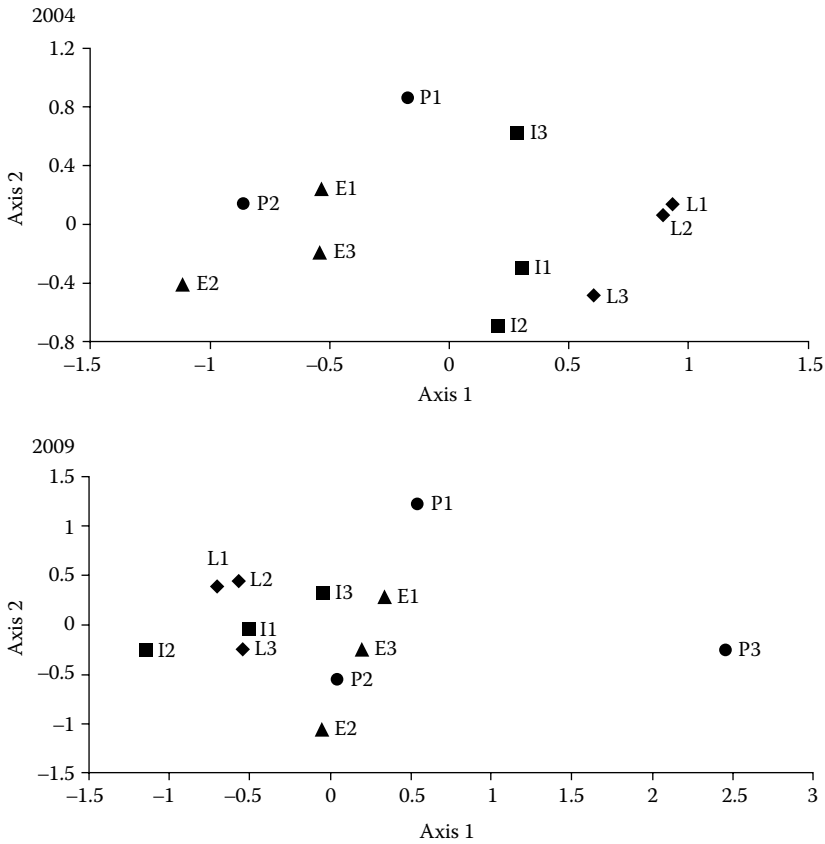
### 2.2.3 Species Composition

Species composition was analyzed by means of a nonmetric multidimensional scaling (NMDS) method that was based on a Bray–Curtis dissimilarity matrix (Figure 2.3). The scores of the axis that explained most of the variation (synthetic variable) were used to compare the successional stages



**FIGURE 2.2**

Species density of Tropi-Dry plots under different successional stages for years 2004 (circles) and 2009 (triangles). P1-P3 = pastures, E1-E3 = early successional plots, I1-I3 = intermediate successional plots, and L1-L3 = late successional plots.



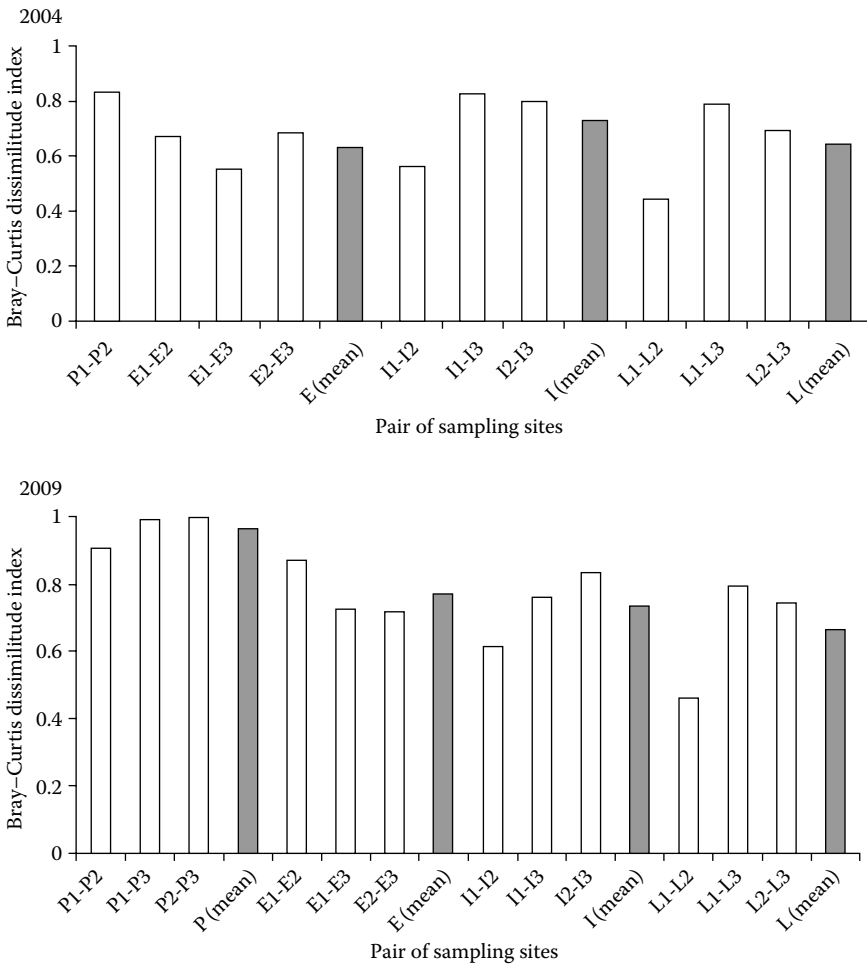
**FIGURE 2.3**

Nonmetric multidimensional scaling (NMDS) of the species composition under different successional stages for years 2004 and 2009. Plots are presented according to their successional stage: circles = pastures, triangles = early, squares = intermediate, and diamonds = late.

in compositional terms. In 2004, pastures and early successional plots significantly differed from intermediate and late successional stages (Pillai test  $F_{(3,7)} = 3.25$ ,  $p = 0.032$ ). In contrast, in 2009, species composition did not differ among the successional stages, suggesting that this parameter became similar to late successional stages in a short period of time (Pillai test  $F_{(3,7)} = 1.51$ ,  $p = 0.237$ ). However, pastures showed great variations in this parameter, and these variations could be masking real differences in the species composition of this successional stage. The great variations among the pastures of the year 2009 (5 years old) again suggest higher stochasticity in the assembly of early successional communities. Stochasticity can be influenced by landscape attributes, as pastures that are separated from the rest of the sites in the analysis are surrounded by pastures; whereas P2, the pasture that is closest to early successional plots in the analysis, is surrounded by secondary

forests (Figure 2.3). Intermediate successional plots of 2009 (13–17 years old) appear more grouped than those in 2004 (Figure 2.3), suggesting a rapid homogenization of plot species composition.

When we analyzed the Bray–Curtis dissimilitude values between the plots, we observed a greater dissimilitude between pasture plots than between plots of other successional stages (Figure 2.4). This suggests that pastures present higher beta diversity than older successional stages. Intra-successional-stage beta diversity should decrease with a decrease along succession in dissimilitude between the plots of a given successional stage. This trend is



**FIGURE 2.4**

Bray–Curtis dissimilitude values between Tropi-Dry plots (open bars) and mean Bray–Curtis dissimilitude values among all the plots of a given successional stage (solid bars) in two different years (2004 and 2009). P1-P3 = pastures, E1-E3 = early successional plots, I1-I3 = intermediate successional plots, and L1-L3 = late successional plots.

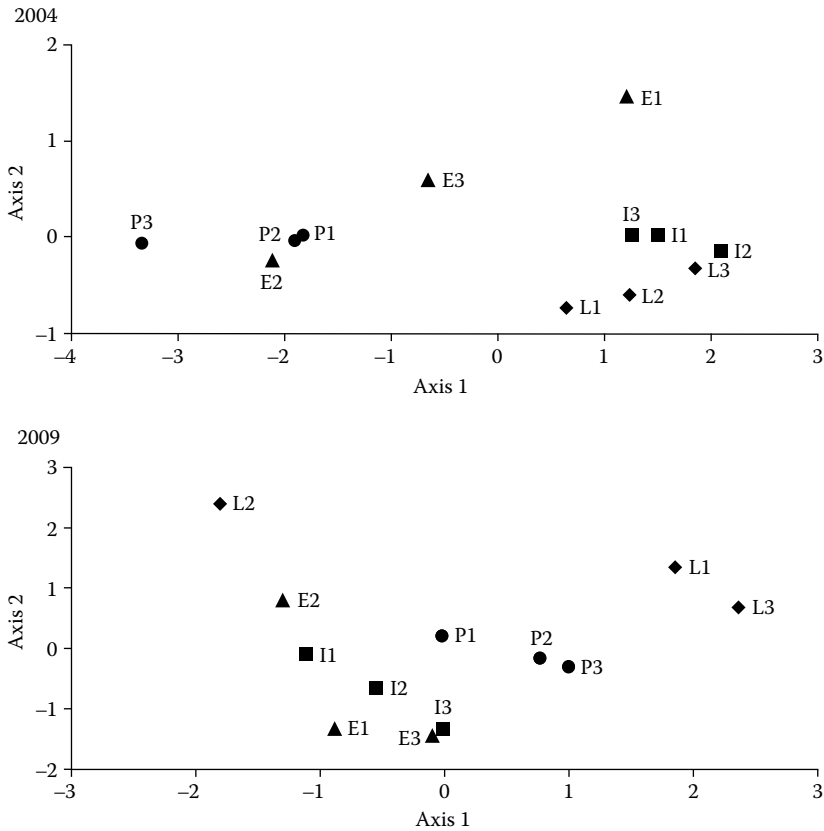
consistent in both years (2004 and 2009). The higher beta diversity in pastures reinforces the idea of greater stochasticity in the assembly of early successional communities, resembling what has been found in other successional models (Leishman and Murray 2001), where stochastic and niche processes dominate early successional stages and only niche processes dominate late successional stages. In these models, both processes have an impact on the community's assembly in the early stages, but deterministic forces dominate the late stages.

#### 2.2.4 Vegetation Structure

Vegetation structure was analyzed through principal component analysis (PCA) (Figure 2.5), which allowed for the ordination of plots in terms of four variables (basal area, number of stems, number of individuals, and number of species). Principal components (i.e., PC1, PC2) that explained most of the variation were used to compare different successional stages through ANOVAs and *post hoc* Tukey's mean separation tests. In 2004, intermediate and late successional plots appeared grouped and separated from the rest of the plots, indicating that structural traits are similar among themselves but different from pastures and early successional stages. In 2009, in contrast, late successional plots appeared grouped along PC1, but there was no clear separation among successional stages along this axis. Intermediate successional plots appeared separated from the rest of the plots along PC2. Most variations in PC2 were accounted for by the number of individuals and the number of species, and parameters were highest in intermediate successional stages. Accordingly, in 2004, ANOVA tests showed significant differences in structural traits among successional stages ( $F_{(3,8)} = 9.835, p = 0.005$ ). Tukey's test showed that intermediate and late successional plots were similar among themselves but different from pastures, whereas pastures were different from all the other successional stages. In 2009, ANOVAs showed no differences among successional stages in PC1 ( $F_{(3,8)} = 1.22, p = 0.365$ ), but significant differences among the stages were detected in PC2 ( $F_{(3,8)} = 4.33, p = 0.043$ ). Tukey's test indicated that, along this axis, intermediate successional plots were similar to late successional plots but different from pastures and early successional plots (which were also similar to each other).

From 2004 to 2009, when the percentage of change in structural variables was analyzed, again, the greatest changes occurred in pastures and early successional plots. The early successional plot E1, however, showed a small increase compared with other early successional sites, probably as a consequence of the high mortality of woody individuals that was caused by an invasion of *Ipomoea* lianas. This mortality reduced the net increase in structural traits. The intermediate successional plot I2 also experienced *Ipomoea* invasion and high mortality, which is reflected in a net reduction in the values of structural traits. In contrast, site I3, which was the youngest intermediate plot, showed the greatest increase during



**FIGURE 2.5**

Principal component analysis (PCA) of the vegetation structure of four successional stages for years 2004 and 2009 in the region of Chamela, Jalisco, Mexico. In 2004, PC1 accounted for 86% of the variation; in 2009, PC1 accounted for 40%, and PC2 accounted for 34% of the variation. Plots are presented according to their successional stage: circles = pastures (P1-P3), triangles = early (E1-E3), squares = intermediate (I1-I3), and diamonds = late (L1-L3).

this successional stage. These cases constitute an example of site-specific effects that can determine particular successional trajectories in different sites of the same region.

In general, late successional plots showed low rates of change for most variables, and most of them showed decreases in the number of individuals and species, indicating mortality of woody individuals. Meteorological data of the Chamela Biological Station over the last 20 years indicate an increase in the number of dry days per year, which could be related to an increase in vegetation mortality (unpublished data). The main structural changes occurred in basal area and stem number, mainly due to increases in stem number and not increases in the number of individuals (as this parameter decreased in most cases). This idea was analyzed through a hierarchical

partitioning analysis, a statistical technique that determines how much of the variation in a given variable (basal area in this case) is explained by other correlated variables (number of stems, number of individuals, etc.). This analysis showed that 93% of the changes in basal area from 2004 to 2009 were explained by changes in stem number (54%), followed by changes in the number of individuals (44%).

The analysis of the ecological succession of a chronosequence of TDFs in Mexico showed that during the first year of the study (2004), pastures and early successional stages were similar to each other but different from later successional stages in terms of species richness, density, and composition. In terms of vegetation structure, early successional stages were similar to intermediate and late stages, as all these stages had an equivalent total basal area. However, this result reflects the high number of small stems derived from the resprouting and recruitment of juveniles in early successional stages. Thus, a casual interpretation of results for total basal area could lead to an underestimation of the time required for structural recovery. Based on what has been stated earlier, the contribution of distinct stem diametric classes to the total basal area should be evaluated. This would enable a more accurate assessment of the vegetation structure at finer scales.

Five years later, in 2009, the four successional stages still differed in most of the variables evaluated, however in a more complex way. Pastures (5 years old in 2009) maintained their distinctness in terms of all the variables analyzed, although they were more similar to early successional stages in terms of species density and structure. Early stages of succession became more similar to later stages in terms of species richness and composition, whereas intermediate and late stages generally remained similar to each other (see results above, [Figures 2.1](#) and [2.3](#)). The increasing similarity in species composition with the advancement of succession is likely the result of a strong effect of deterministic factors. In contrast, stochastic factors, which appear to be important in explaining intersite variations in pastures, become less relevant in later stages of succession. It is of particular importance to state that the composition and structure of intermediate and late successional stages are similar from the beginning to the end of the chronosequence study, indicating that management practices that occurred in the intermediate stages maintained many species and trees in disturbed areas.

Although it appears that species composition is similar between intermediate and late successional stages, less frequent and rare species are not likely to be similar in both stages. For instance, other studies have demonstrated that beta diversity is high in mature TDFs in the region (Lott and Atkinson 2002; Balvanera et al. 2002), creating a heterogeneous landscape. In addition, the most diverse plant community of Chamela–Cuixmala, which is found in the canopy stratum (lianas, orchids, and bromeliads), is likely to be one of the communities that is most affected by disturbance, although this idea has not been assessed in the context of succession. However, a study of epiphyte-host networks in the Chamela–Cuixmala region in Mexico showed

that the assembly of these commensalistic interactions is determined by the host-species abundance, species spatial overlap, host size, and wood density (Sáyago et al. 2013). Only the host plant communities of late successional stages are capable of supporting the unique, diverse canopy plant community of Chamela–Cuixmala. Further work on the succession of TDFs should include an analysis of all canopy-level strata. Meanwhile, it is important to interpret results from vegetation analyses with caution and to critically evaluate apparent similarities among successional stages that may reflect different underlying processes or causes.

---

## 2.3 Phenology

Phenological data were collected during four years (2006–2010) for a total of 695 individuals who belonged to 90 species. Results for this part of the study are presented in detail in Chapter 7 by Lopezaraiza et al.; next, we present a summary of the major findings of this study.

### 2.3.1 Leafing

All successional sites showed a distinct and consistent leafing pattern both within and across years. The months with the highest proportion of individuals with no leaves were April, May, and June. During the drier months, the proportion of individuals and species with no leaves was higher in the late successional sites. During the greener months, there was no difference among successional stages in the proportion of individuals or species with 50%–100% leaves. In the late successional sites, a higher proportion of individuals had no leaves for five or more months in a year; whereas at early and intermediate sites, a higher proportion of individuals maintained their leaves for six or more months per year. Thus, in general, individuals keep their leaves for longer at the early and intermediate sites.

### 2.3.2 Flowering and Fruiting

General patterns of flowering and fruiting at the community level show peaks at different times of the year. This may be due to differences in community composition and species abundance among plots, as well as due to the differences in the local physical environment. Almost every month, at least one species is flowering or fruiting, with large variation among sites. The most consistent flowering peak across sites and years occurs at the end of the dry season and at the beginning of the rainy season, around the months of June and July. There are other flowering peaks at different times for various sites at the end of the rainy season and at the beginning of the dry season.

At the early and intermediate successional sites, some individuals flowered for three to five months in a year; whereas at the late successional sites, individuals were only recorded flowering for one or two months in a year. In contrast, at the early successional sites, individuals were recorded with fruits for approximately three months in a year; whereas at the intermediate and late sites, some individuals were recorded with fruits for 4 to 10 months in a year. Thus, individuals tend to flower longer at early successional stages, whereas they ripen or bear fruits longer at late successional stages.

---

## 2.4 Successional Changes in Vertebrate Communities

In this study, we analyzed mainly bird and bat communities along successional stages.

The chapter by Nassar et al. (Chapter 11) and the studies by Avila-Cabadilla et al. (2009, 2012) describe the main findings of this section in detail.

### 2.4.1 Birds

In total, we captured 2,775 individuals of 84 different species. The most abundant species were *Vireo flavoviridis* (12.3%), *Passerina lechanclerii* (11.29%), *Cyanocompsa parellina* (11.03%), and *Columbina passerina* (9.4%). Fifty-one species were considered rare, because they occurred at low abundance (<0.5% of total captures). When comparing bird species richness and diversity among successional stages, the stages did not differ significantly in terms of rarefied species richness (Kruskal–Wallis tests  $\chi^2 = 3.77$ ,  $p = 0.28$ ) and rarefied Shannon diversity indices ( $\chi^2 = 1.33$ ,  $p = 0.72$ ). However, bird species composition differed between late successional plots and the remaining successional stages when analyzed through NMDS. Species composition among plots that were evaluated through the Morisita index showed a gradient of similarity along successional stages, where pastures were more similar to early successional sites, and intermediate sites were more similar to late successional sites. A comparison of plots through rank-abundance curves showed some species that occurred exclusively in particular successional stages. These species could potentially be considered indicator species. In general, our results suggest that the mosaic of secondary forests characterizing this region plays an important role in the maintenance of bird species biodiversity.

### 2.4.2 Bats

We documented the changes in the structure of bat assemblages among the secondary successional stages of Chamela–Cuixmala TDF over 42 nights of sampling and captured 606 phyllostomid bats belonging to 16 species.

In general, the late stage had the highest species richness, sustaining all 16 species, followed by the intermediate site with nine species, and the pasture with four species. Species found within any successional stage were a combination of species found at the previous stage as well as additional species. Bat diversity and abundance did not differ significantly among early, intermediate, and late stages. However, nectarivores were more abundant in early stages than in late stages, likely as a consequence of differences in food availability. Our results suggest that areas of forest that are recognized as late successional are the most important reservoirs of species richness.

We also evaluated variations in the occurrence of phyllostomid bat assemblages in different successional stages and variations in relation to habitat attributes at local (vegetation structure complexity) and landscape levels (percentage of forest cover, mean patch area, and diversity of patch types). We found that frugivore abundance was mainly explained by variations in the amount of riparian vegetation, whereas nectarivore abundance was mainly explained by variations in the amount of dry forest vegetation. These results reflect that fruit resources for bats mainly occur in the riparian habitat, whereas bat floral resources are mainly found in the dry forest habitat. We conclude that the preservation of the riparian vegetation is crucial for the conservation of bat diversity and the important ecological interactions in which bats are involved in TDF-transformed landscapes.

---

## 2.5 Human Dimensions

Humans have inhabited the coast of Jalisco for thousands of years (Mountjoy 2008). Before the Spaniards' arrival, indigenous communities had low impacts on the ecosystems of the region and even during early colonial times, the region remained relatively undeveloped (Rodríguez 1991). Eventually, the colonists directed the conversion of indigenous people's lands into extensive Haciendas that were dedicated to cattle ranching and agriculture, which led to land disputes that lasted over centuries. The coast of Jalisco was characterized by the presence of extensive Haciendas. Today, the Chamela–Cuixmala Biosphere Reserve is surrounded by Ejidos (see Chapter 21). During the 1950s, the federal law of Mexico promoted the colonization of the Pacific coast. This policy sparked TDF transformation in the Jalisco coastal region and land-ownership conflicts that have lasted until the present day. For many decades, government policies considered forested areas as useless lands, promoting the destruction and conversion of TDFs into pastures for cattle ranching and agricultural fields. Over time, governmental policies did not produce the expected results. On the contrary, TDFs have been cleared and fragmented, and local families have not accomplished dignified livelihoods. For example, in the Ejido Ley Federal de la Reforma Agraria, 70% of Ejido's

young men migrate to the Americas in search of job opportunities. These migrants send a monthly stipend to their families, and this has become the most important source of income along the coast of Jalisco.

When we query the local population on their perceptions of policy outcomes, the opinion of local Ejidatarios is that government policies only favor those who are in better economic positions or investors who are interested in developing the coast for tourism. The current Coast of Jalisco Land Use Planning Program—a program that enhances social development and biological conservation in the region—prohibits clearing land for agriculture and favors private investment (Castillo et al. 2009). Most Ejidatarios disagree with these policies. Our analysis also reveals that, although the conservation of TDFs is clearly necessary to preserve biodiversity and ecosystem services, many local people are in conflict with conservation policies. Local and federal governments have favored land concessions to national and foreign investors to develop large-scale tourism projects that promote socioeconomic injustice and environmental damage. People recognize the need to create policies that regulate large-scale exploitation of TDFs and coastal resources by a few stakeholders and to preserve TDF habitats and ecosystem services.

---

## 2.6 Conclusions and Recommendations

Our study showed that secondary TDF succession is not a simple, unidirectional linear sequence of change in functional groups/species composition. In general, the analysis of the ecological succession of a chronosequence of TDFs in Mexico showed that, after five years, pastures maintained their distinctness in terms of all composition and structure variables analyzed, although they were more similar to early successional stages in terms of species density and structure. Early stages of succession became similar to later stages in terms of species richness and composition, whereas intermediate and late stages remained similar to each other. The increasing similarity in species composition with the advancement of succession is likely the result of strong deterministic factors. The composition and structure of intermediate and late successional stages are similar from the beginning to the end of the chronosequence study, indicating that management practices in the intermediate stages maintain many species and trees in disturbed areas. Although it seems that species composition is similar between intermediate and late successional stages, the high beta diversity found in the plant communities of the TDFs of Mexico indicates that less frequent and rare species may not be similar in both stages, and a more heterogeneous landscape should be found at a larger scale. Further research should identify the main dynamics involved in TDF succession to develop models of recruitment dynamics of

key dry forest plant species that facilitate the process of succession following natural or human-induced disturbances.

One component of TDFs for which an assessment of succession has not been conducted is found in the canopy stratum (lianas, orchids, and bromeliads), which encompasses the most diverse plant community of the Chamela–Cuixmala region. Changes in vegetation attributes in this forest stratum are likely to differ greatly with succession. Specifically, a decrease in species composition in early and intermediate successional stages would be expected due to a reduction in host species abundance, host size, and wood density (Sáyago et al. 2013). Apparently, only the host plant communities of late successional stages are capable of supporting the canopy plant community of the Chamela–Cuixmala TDFs. Further work on the succession of TDFs should include an analysis of all canopy-level strata. Meanwhile, it is important to interpret results from vegetation analyses with caution and to critically evaluate apparent similarities among successional stages that may reflect the different underlying processes or causes.

Another important aspect to be considered in the process of ecological succession is the functional response of the community, in which certain groups of plants and animals respond in a similar fashion to environmental conditions and are associated with particular successional stages. Preliminary data from our study in Mexico indicate that certain plant groups that share specific plant functional traits are more likely to be represented in a particular successional stage. For example, groups of plants in early successional stages that are more exposed to high temperatures and solar radiation tend to maximize heat dissipation more than plants from late successional stages, which tend to enhance more light acquisition and water use. Therefore, the functional recovery of TDFs might be more complex than inferred by just analyzing floristic and/or structural components of the community. In addition, the variations in animal community assemblages also seem to be associated with different successional stages. Our studies show that bird and bat guilds tend to be more associated with certain habitats under certain successional stages. More studies from other tropical regions are required to corroborate patterns of functional succession. In conclusion, the main mechanisms of succession and regeneration of TDFs still remain unexplored, and more efforts are required to understand the ecological processes of these important ecosystems.

Another important process to consider in ecological succession is related to plant phenology. Phenological differences encountered among successional stages might be related to biophysical parameters in which early successional stages should show high canopy openness (high light transmission) and low Leaf Area Index as a consequence of their low vegetation density and plant cover. This, in turn, should be reflected in low water availability, high light availability, and high temperature. Some of these environmental events have been proposed to trigger phenological patterns in plants. Leaf flushing is a phenological process that is directly associated to primary productivity.

The timing of leaf flushing is similar in all successional stages, but early and intermediate stages appear to retain leaves longer than do late successional stages. In addition, early successional stages also maintain flowers all year round with higher peaks of fruiting as well. It seems that plants in early successional stages are capable of using high light environments with high water efficiency and are very effective at temperature regulation. Extended patterns of flowering phenology in early successional stages are likely to maintain pollinators, particularly bees and butterflies, for long periods of time. Future research should be designed to study how intraspecific variation in the frequency, duration, amplitude, and synchrony of flowering may affect the reproductive success and genetic structure of plant communities in relation to the regeneration capacity of the different successional stages.

Finally, our study showed that human settlements have transformed a part of the landscape surrounding the Biosphere Reserve, but a high percentage of mature and successional forest is still found in fragments and continuous patches, which are owned by the communal land ownership of *Ejid*os. Although this Biosphere Reserve is still surrounded by an almost continuous forest, this important protected area of Mexico may turn into an island in less than 50 years at the current rate of deforestation, especially if trends related to *Ejid*os lands, private ranches, and urban developments far from the Biosphere Reserve are maintained (Sánchez-Azofeifa et al. 2009a). *Ejid*os encompass 70% of the territory located in the vicinity of the Biosphere Reserve, and the remaining land is divided between tourist developments and private properties. *Ejid*os are also characterized by poverty, high levels of illiteracy, migration, and limited access to secure employment. Agricultural production is the main economic activity, but it cannot secure peasant families' livelihoods. Although peasants recognize the services provided by TDFs, such as cooler climate, shade, and plant and animal species for family consumption, they are proud of their pasture fields and economic activities that are aimed at creating jobs and reducing migration to the Americas. Consequently, the conservation and restoration of TDFs is not perceived as a necessary activity, as has been found in interviews carried out in this study. As a communal tenure forum, *Ejid*os have a social organization that helps the conduction of collective activities such as forest exploitation. Their organization is also positioned with the local social institutions with which a regional conservation and development plan can be formulated and implemented.

New strategies for the preservation and restoration of TDFs should promote conservation via payment for environmental services. Among the most important environmental services are (1) pollination of crops by wild pollinator species, a service that is particularly important for temporal crops grown in riparian habitats; (2) protection of watersheds and aquifers, a service that helps prevent natural disaster and ensures availability of one of the most essential and endangered natural resources—water; and (3) carbon sequestration by mature and regenerating forests, a service that provides a



healthy environment for tourists and local communities, while contributing to a reduction in the impacts of global climate change. Consequently, to accomplish the goal of promoting conservation through environmental services, we propose the creation of a “Red de Areas Ejidales Protegidas” (Ejidos’ protected areas network) in the region surrounding the Chamela–Cuixmala Biosphere Reserve (Sánchez-Azofeifa et al. 2009a). In this network, Ejidos will commit to protect land within their property, and the government and the Biosphere Reserve will commit to pay for environmental services and to provide technical assistance and training for alternative ecosystem management strategies. For this to be implemented, the government agency that is responsible, along with the Biosphere Reserve, should accept a leading role in the construction of a payment form that improves peasant families’ livelihoods and secures the long-term maintenance of TDFs and associated habitats. Promotion of environmental educational programs and training activities for the Ejidos should be implemented to modify the way in which they perceive and value TDFs. Furthermore, a continuous communication exchange between the Ejidos and the Biosphere Reserve should be enforced. Research groups and institutions would also play an important role in terms of providing information for evaluating the services provided by the Ejidos’ reserves. Schemes similar to those developed in countries such as Costa Rica (Sánchez-Azofeifa et al. 2007) may be used as an initial template. The implementation of economic schemes under programs for payment of environmental services will be a very dynamic way of pragmatically enforcing sustainable development, conservation, and management in tropical rural Mexico.