

**Diversity patterns of herbaceous angiosperms along
gradients of elevation and forest use intensity in
Central Veracruz, Mexico**

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Summary

Terrestrial herbs are an important element in tropical forests; however, there is a lack of research on their diversity patterns and how they respond to different forest use intensities. Studying the richness and distributional patterns of this group along elevational gradients is important in order to understand the general processes that influence this distribution. Previous investigations have been done on elevational gradients and the effect of land use intensity on plant diversity, however, relevant research on herbaceous angiosperms is still scarce compared to other groups of vascular plants, such as trees. In order to bridge this gap, I studied herbaceous angiosperm distributions along gradients of elevation and disturbance. Therefore, the study of an elevational gradient proposed in this work provides an opportunity to analyze distributional patterns of herbs in a tropical area with contrasting environmental conditions. It is important to notice that this is the first study of its class on Mexico.

First, we analyzed species richness and floristic composition of herbaceous angiosperms at eight elevational sites (Chapter two). We compared those patterns with respect to land use intensities at Cofre de Perote, central Veracruz, Mexico. We established an elevational transect (40 to 3,520 m) where we recorded the occurrence of terrestrial angiosperm herbs within a total of 135 plots of 20 x 20 m. We compared species richness and floristic composition between the different elevational belts and degrees of forest disturbance. We recorded a total of 264 herb species, 31 endemic to Mexico and three classified as threatened. The total number of species represents 5.7% of species of the Veracruz' herbaceous angiosperm flora. The elevational belts with highest species richness were 2,500 m (76) and 1,500 m (52). In most cases, secondary forests showed the highest species richness along the elevational gradient, whereas old-growth forests had fewer species. The observed species richness, including endemic elements, highlights the importance of plant conservation in areas threatened by land use changes. Additionally, we suggest that environmental heterogeneity formed by mature, disturbed and secondary forests is acceptable (and unavoidable) and can even increase species richness.

Second, we described the influence of elevation and forest use intensity on alpha, beta, and gamma diversity along gradients of elevation (50 m to 3500 m) and human forest use intensity (Chapter three). We analyzed species richness and floristic composition in six vegetation belts at different elevations and in different habitats. We found some general elevational trends, such as the increase in α -diversity and β -diversity and a decline in β w-diversity. Also, γ -diversity follows a hump-shaped pattern with a peak between 2500 m and 3000 m and a decrease at the extremes of the elevational gradient. There was no effect of forest use intensity on α -diversity, only β -diversity increased depending on the change of habitat with the highest values when old-growth forest are transformed into secondary forests. Therefore, a loss of a specific forest area is compensated by the occurrence of a similar assemblage at other areas of the same location. The observed high β -diversity, including endemic elements, suggests that a mix of different habitats is needed for reaching high γ -richness of terrestrial herbs.

Third, we described the deforestation and fragmentation patterns of the study area during three different time periods (1993, 2000 and 2014; Chapter four). We quantified the net change in forest area and the loss of original forest area. Our results showed a reduction in the area of the original vegetation by about 57%. The annual net forest change rate for the first period (1993-2000) was -0.44%; and increased significantly to 0.11% for the second period (2000-2014). The old-growth forests of Central Veracruz have suffered high rates of land use change throughout the last twenty years with a reduction of this process during the last decade. In the first period, forest patches increased in irregularity, isolation and size with a reduction in the dimension of the fragments that represented the destruction of natural vegetation, whereas the second period experienced a slightly recovering of forest cover (0.11%). This chapter provides a thorough analysis of the forest transformations in Central Veracruz that will increase the consciousness of stakeholders for proper planning and management to maintain biological integrity of the area.

Finally, I synthesize the principal findings of this thesis and highlight the implications for conservation. Also, I suggest potential topics be studied in the future with the data obtained, related with remaining forest and alpha and beta diversity patterns of endemic herbs (Chapter five).

CHAPTER 1: General introduction



Humid montane old-growth forest in *El Zapotal*, Veracruz, Mexico at 2000 m.

1 General introduction

1.1 Plant diversity and distribution along elevational gradients in the tropics

The knowledge about the distribution of herbaceous angiosperms along elevational gradients worldwide is still scarce as only a limited number of extensive studies have been conducted. For example, in a transcontinental comparison, Cicuzza *et al.* (2013) studied the distributional patterns of tropical herbaceous angiosperms. They found that the local difference of herbaceous angiosperms species richness is influenced by factors such as temperature, elevation, and actual evapotranspiration. Additionally, they found that elevation promotes the herbaceous angiosperm richness but there was no relation with precipitation. They did not find a clear explanation for that pattern but suggested that apparently the effect of higher moisture in highlands, as well as evolutionary legacies, could explain it. In general, the treeline marks the limit of herbaceous angiosperm richness with a decrease close to and beyond this area (Wesche *et al.* 2008).

Desalegn & Beierkuhnlein (2010) investigated at the landscape scale the mechanism that drives the structure of herbaceous diversity in the Southwest Ethiopian mountains. They found that herbs presented a cumulative increase tendency from 1100 to 1500 m, a decrease at mid-elevations (1500-2000 m) and then a constant increase to upper elevations. They attributed that the herbs did not show a hump-shaped pattern due to the effect of an incomplete gradient. Therefore, from whole explicated variance, elevation had explained a low proportion of the variance (16%) and the change in bedrock, as an indicator of the nutrient gradient, explained 27% of the variance for herbaceous diversity.

In a global meta-analysis, Nogués-Bravo *et al.* (2008) analyzed 37 elevational species richness gradients in a range from 0 to 6000 m of terrestrial plants finding that the most common pattern of diversity is the hump-shaped (76%), followed by decreasing diversity with elevation (16%). In the case of the hump-shaped pattern, the peak of diversity was in average at 1364 m (SD \pm 531 m).

Along an elevational gradient at the Mt. Kilimanjaro, Hemp (2005) recorded 858 herb species (70% of the total vascular plant richness). The peak of species richness was found

at 1700 m and most of the variance was explained by elevation ($r= 0.91$), mean annual temperature ($r= 0.87$), mean annual minimum temperature ($r= 0.86$) and pH ($r= 0.81$).

There are few studies realized in the Neotropics (Fig. 1.1), for example in Ecuador, along with a gradient from 1850 to 3000 m, where Homeier *et al.* (2013) studied the factors that are involved in the diversity patterns. They found 552 species at the lowest part of the gradient (*ca.* 1850 m), which was the site with highest species concentration. The authors explain that soil nutrient concentration and geographical gradients of some abiotic factors such edaphic, precipitation and landform conditions appear to be the major factors determining differences in elevational locations.

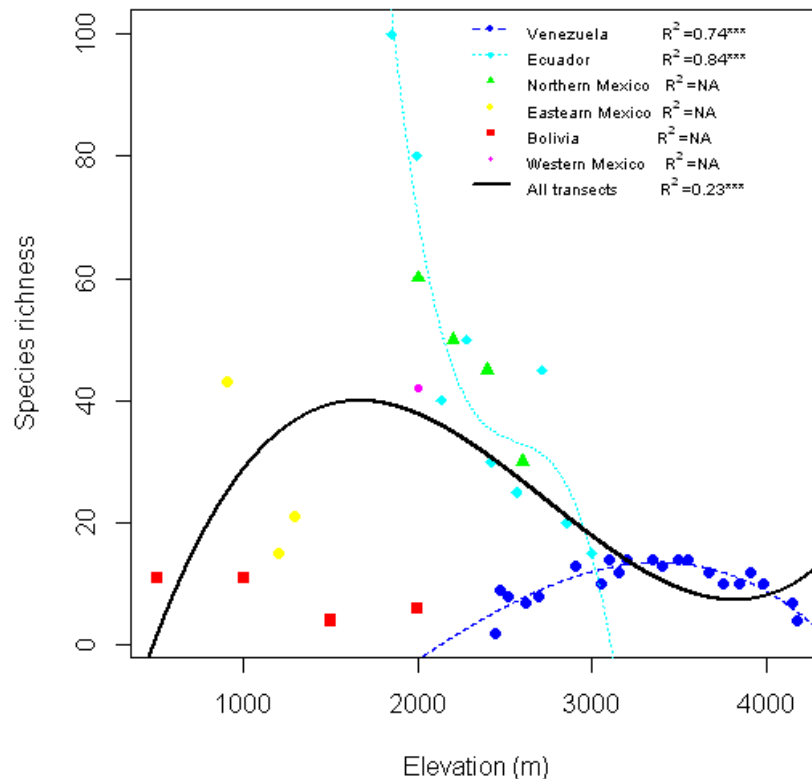


Figure 1.1 Elevational patterns of herbaceous angiosperm diversity in the Neotropics based on the following studies: Bolivia (Kessler *et al.* 2000), Ecuador (Homeier *et al.* 2013), Northern Mexico (Encina-Domínguez *et al.* 2007), Eastern Mexico (Krömer *et al.* 2013), Western Mexico (Vázquez & Givnish 1998), and Venezuela (Márquez *et al.* 2004). The black line marks the general pattern of the six combined transects.

In Venezuela, Márquez *et al.* (2004) studied the distribution of grasses along an elevation gradient between 2500 and 4200 m. They found 47 grass species along the gradient, with a richness peak at ca. 3500 m (Fig. 1.1). They attributed the elevational pattern to the phytogeographical origin and abiotic processes, such as low temperatures, high incoming radiation, water stress and slope aspect.

In Bolivia, Kessler *et al.* (2000) studied selected plant groups along an elevational gradient from 500 to 2450 m. They found 32 species of herbaceous angiosperms and a linear decrease of species richness with elevation (Fig. 1.1). They attributed the decrease of species richness to the high frequency of night frosts.

In western Mexico, Vázquez & Givnish (1998) studied several plant groups along an elevational gradient from 1500 to 2500 m. They found 181 terrestrial herbs with a peak of 42 species at 2000 m (Fig. 1.1). Understorey herbs were negatively correlated with elevation, the authors hypothesized this pattern due that at drier and lower elevations the habitats have more totally deciduous canopies and are more exposed to disturb. Likewise, elevation affects soil fertility and anti-herbivore defenses which can drop the diversity with elevation.

Encina-Domínguez *et al.* (2007) along with a gradient in Northern Mexico from 1590 to 3140 m recorded 171 herbs. The authors found a high diversity in mid-elevations (2100 m) due to the border effect of the transition areas between plant communities (Fig. 1.1). Also, they attribute the high herb richness to the migrant effect, which is explained by the immigration of species between two different forest types. Finally, they also found a high beta-diversity attributed to a high environmental (climatic and edaphic) heterogeneity associated with the relief.

In the state of Veracruz, Eastern Mexico, Krömer *et al.* (2013) studied the effect of elevational locations area and climate on herb richness. They studied five taxonomical assemblages along three elevational gradients finding 50 herbaceous angiosperms. The elevational pattern depended on the taxonomical group, with specific groups that presented important variations related with elevation: Araceae presented a decrease with elevation, whereas there was an increase of Orchidaceae and Piperaceae (Fig. 1.1). The authors suggest to separate different groups of terrestrial herbaceous angiosperms in

order to obtain more clear elevational patterns and that herb layer is more related to bryophyte cover and precipitation.

All of these studies related the diversity and distribution patterns of herbaceous angiosperms with environmental variables (climate or precipitation) present along the elevational gradients. There are few works that include the impact of human influence on the biotic communities, as done by Kessler *et al.* (2001), which verified that herbaceous species are negatively affected by human disturbance. As well, Jácome-Reyes (2005) related the structure and composition of high montane herbs with temperature and elevation along an elevational gradient in Bolivia. They found that climate change and human disturbance in these zones might lead to variations in the dominance arrangements and an increase of invasive species from neighboring zones.

In studies concerning the anthropic impact on herb diversity (Cicuzza *et al.* 2011), those studies found that the systems with a high disturbance degree present an increase in total species richness and showed a considerable increase in richness in less disturbed forest-use categories. However, in more disturbed forest-use categories, the richness widespread species was increased. Therefore, herbs were influenced by traits that control their range sizes in response to anthropological events (Lozada *et al.* 2008). Under extremely degraded environment circumstances, widespread herbs tend to display strong competitiveness, which is the reason why there is a dominance of such herbs in extremely interfered forest-use categories and the most sensitive group to degradation are the species with narrow ranges form (Kessler 2001). It is also known that human-intervened agroecosystems preserve many narrow-ranged species (endemics) and can contribute considerably to general species richness (Lozada *et al.* 2008).

The above-mentioned works give an overview of the arrangements of herb diversity along elevational gradients in the tropics; however, the available information is not concluding due to the high variation in different organism groups and several world regions (Cicuzza *et al.* 2013), therefore it is actually not possible to determine a general elevation pattern of herbs (Fig. 1.1). Even as shown in figure 1.1 there are contradictory patterns on elevational gradients, on one hand, there is an increase in species richness with elevation and on the other hand, the contrary occurs on other elevational gradients. Furthermore,

there is even less information about the impact of human disturbance on the diversity and distribution patterns of herbaceous angiosperms under different biotic and abiotic conditions presents along an elevational gradient.

1.2 Deforestation as driver of species richness loss due to forest use alteration

Some of the main contributors to global climate change are the decrease in carbon sinks and forest loss which increase the atmospheric concentration of CO₂ (Houghton *et al.* 2000). After fossil energy combustion, deforestation is one of the most important human causes of increasing CO₂ emissions to the atmosphere (approximately 6 to 17% of world emissions) (van der Werf *et al.* 2009). Hansen *et al.* (2013) found that in the period from 2000-2012 there was a loss of 2.3 million km² (slightly neutralized by an increase of 0.8 million km²) of forests worldwide. The tropical rain forest ecozones in Southeast Asia, Africa, and Latin America are the greatest endangered forest portions of the world (Saatchi *et al.* 2011). The loss of forest area in Latin America is one of the main losses globally (Achard *et al.* 2002). At the national level, Mexico possesses 2% of the total carbon deposited in tropical forests but produces too emissions due to forest loss (Baccini *et al.* 2012). Around 2% of the total carbon emissions (8 Tg C yr⁻¹) of Latin America took place in Mexico, where the current research took place, in the period from 2000-2005 (Harris *et al.* 2012) and had a total forest cover loss of 24 Mha in the 2000-2012 period (Hansen *et al.* 2013), which has made Mexico the 11th main worldwide emitter of CO₂ (1.4% of world emissions) to date (The World Bank 2016). The Yucatan peninsula, Veracruz, and Chiapas are the areas where forest loss is happening to a high rate (Fig. 1.2).



Figure 1.2 Deforestation in Mexico between 2000 and 2014 (Hansen *et al.* 2016). Source: Hansen/UMD/Google/USGS/NASA. Data available online from <http://earthenginepartners.appspot.com/science-2013-global-forest>

Numerous ecosystem services are provided by tropical forests such as regulation of the global climate system, carbon sequestration, and protection of soil. In addition to water filtration, conservation of species richness, renewable energy, and resources (Foley *et al.* 2005). In general, the logged zones are transformed into agrarian farming schemes (Achard *et al.* 2002), which causes the alteration on the provision of significant ecosystem services and an enormous loss of species richness in these areas. Tropical forest ecosystems are home to some of the highest concentrations of rare species in the world and have a remarkably high biodiversity (Myers *et al.* 2000).

Latin America has seven of the 25 global biodiversity hotspots defined by Myers *et al.* (2000). The state of Veracruz, Mexico, where the present research was done, is located

in one portion of the Mesoamerican hotspot. Extremely rare species have evolved in Mesoamerica due to its exceptional geological history, as well as its diversity of climates and the confluence of the neotropical and nearctic regions (Harvey *et al.* 2008). However, large areas of natural forests are cleared for agricultural purposes and cattle pasture areas (Fig. 1.3 A), which made Veracruz the main producer of cattle inside the country encompassing around 11% of Mexico's cattle production (INEGI 2007).

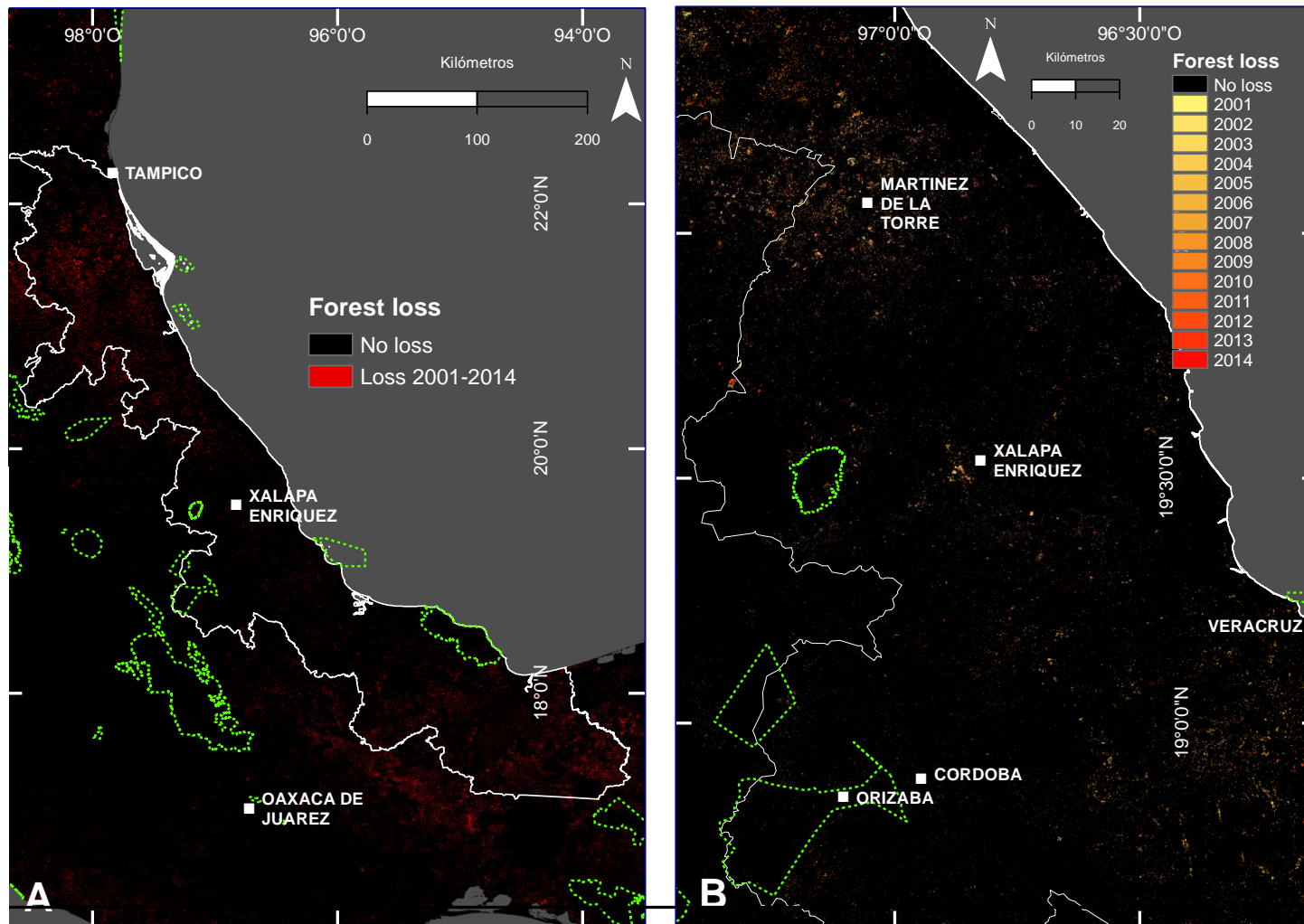


Figure 1.3 Forest cover loss in Veracruz, Mexico. A) Total forest loss from 2001-2014 in Veracruz. B) Yearly deforestation between 2001 and 2014 in the study area central Veracruz, protected areas are shown (green line). Source: Hansen/UMD/Google/UGS/NASA (Hansen *et al.* 2016). Data available on-line from <http://earthenginepartners.appspot.com/science-2013-global-forest>

The region of central Veracruz includes relicts of two rare forest ecoregions within a biodiversity hotspot, i) the humid montane forest with an area of about 4,069 km² of which only 4% is part of protected areas (Gillespie *et al.* 2012, Williams-Linera 2013), and ii) the dry forest with an area of about 372 km² where only 2% is protected (Gillespie *et al.* 2012, López-Barrera *et al.* 2014) (Fig. 1.3 B). However, increasing forest conversion into cattle pastures and agricultural fields still presents the main pressure to the natural forest in this area. In addition to tropical forest loss and transformation, additional stress on species richness is exerted through landscape homogenization. The previous as result of logging and an increase of current agrarian areas by rises in inputs of fertilizers and herbicides (Benton *et al.* 2003). Veracruz has one of the highest forest loss rates in Mexico and to date, most of the natural forest has been transformed mainly into agriculture and cattle areas (Table 1.1). It is estimated that if the current tendency continues by the year 2020 only 1% of the natural forests will remain.

Table 1.1 Changes in land use coverage in Veracruz for the period 1971-2020 (INEGI 2000, Ellis & Martínez 2010, Gerez-Fernández & Pineda-López 2011).

Land cover	1972 (%)	1981 (%)	1984 (%)	1993 (%)	1994 (%)	2000 (%)	2007 (%)	2020* (%)
Forests	41	38	20	19	19	18	9	1
Agriculture	27	26	37	35	31	28	33	34
Cattle	22	24	34	32	34	47	46	51
Secondary forests	7	8	6	9	11	4	7	9
Grassland	2	3	2	3	3	2	3	3
Other	1	1	2	2	2	1	2	2

* The values for the year 2020 were estimated based on Gerez-Fernández & Pineda-López (2011) values.

Considering the huge quantity of carbon deposited and their remarkably high species richness, forest loss in Mesoamerican ecosystems has the potential to promote grave world-wide consequences on species richness and climate (de Albuquerque *et al.* 2015). There is a continuing discussion whether land should be definitely chosen “for nature” and “for production”. Consequently, it can generate a separation (land sparing) through agrarian intensification (high input-high yield) or whether a more combined method to land use should be accepted e.g. following wildlife-friendly agricultural (low input-low yield) (Gilroy *et al.* 2014, Abou Rajab 2016).

Deforestation and land use change have different consequences on the diversity of herbaceous angiosperms. However, studies on this subject are scarce and to date, there is no research made on the effect of forest use intensity on herbaceous angiosperms in Veracruz.

1.3 Herbaceous angiosperms as a study model

Herbaceous angiosperms of the forest understory are defined as non-woody or only slightly woody plants that are rooted on the forest floor (Poulsen 1996), including facultative terrestrial species like hemiepiphytes that are only at ground level for part of their life cycle (Cicuzza *et al.* 2013). These plants form a functional guild that exploits the same class of resources sharing traits (Stroud *et al.* 2015). Also, this guild is one of the most widespread angiosperm groups in the world, owing to their plasticity in habitat and reproduction form (Hawkins *et al.* 2011). This group has the largest number of exclusive families in the angiosperm phylogeny (37%) with at least 149 families unique to being herbaceous (Hawkins *et al.* 2011). Furthermore, these plants occur in a variety of habitats, from rainforests to deserts, rugged mountains to savannas, farmlands and even suburban and urban landscapes (Hawkins *et al.* 2011).

The assemblages of trees and herbs vary considerably on traits, rates of phenotypic and molecular evolution (Smith & Beaulieu 2009). For example, woody lineages have fewer variations per million years in climatic niche space than associated herbaceous plants and climate space exploited by herbs is higher than parallel lineages composed mostly of

woody groups (Smith & Beaulieu 2009). In some cases, the differences on niche between herbs and woods might just be related to geography as in the case of Primulales (Smith & Beaulieu 2009).

The maximum richness of herbaceous angiosperms can be found in tropics, northern latitudes (45°), mainly in the Nearctic and portions of the North Temperate Region. In general, the average herbaceous angiosperm range sizes have a tendency to be comparatively small in northern California, eastern USA and the tropics (Hawkins *et al.* 2011). Herb families are younger on average in the north tundra region, Tierra del Fuego, the Australian and Sahara deserts, but are not particularly ancient in the tropics (Hawkins *et al.* 2011). Herbs are responding adaptively considerable more intensely to present climate than to previous one (Hawkins *et al.* 2011).

There is no phylogenetic relationship of important traits within herbaceous angiosperms because trait evolution amongst them is occurring so fast (Hawkins *et al.* 2011). Herbs are adapted to cold climates and had a success on temperate zones due to be annual and the production of underground structures (e.g. rhizomes and stolons) (Hawkins *et al.* 2011). Assuming that there is no sign of family level niche conservatism with respect to cold climates, it is interesting that the newest families of herbaceous angiosperms had originated in the aridest environments (Hawkins *et al.* 2011).

Herbaceous clades are evolving rapidly with numerous important traits, this fast process of evolution might reveal a faster rate of adaptation to varying climatic conditions. As an example of this procedure, it can be mentioned the increase of the ecological dominance of C₄ grasses in lower latitudes (Edwards *et al.* 2010).

Furthermore, understory plants in tropical forests comprise around 45% of the vascular plant species richness (Linares-Palomino *et al.* 2009, Cicuzza *et al.* 2013). Terrestrial herbaceous angiosperms are frequently slightly unequally dispersed on the tropical forest floor, and species with underground stems or buds are common (Richards 1996). Furthermore, within the understory herbs monocotyledons (monocots) are the most prominent group, which have some adaptations to drought like diffuse root structures deprived of one or few central roots. This different architecture affects the mode in which the herbs absorb water and nutrients (Robinson 1994). The mean annual precipitation of

the driest month is negatively linked to dicots diversity, as reported by Cicuzza *et al.* (2013), explained to their morphological and physiological adaptations (Willinghöfer *et al.* 2011). The study of Cicuzza *et al.* (2013) recovered indicator herbaceous angiosperms families that on particular continents play the main role (Table 1.2).

Table 1.2 Indicator herbaceous angiosperms families found in tropical transects worldwide adapted from Cicuzza *et al.* (2013). Families registered are considerably well represented in respective continent transects than in those of the other two contents (* Monocots, ** Dicots).

America	Africa	Asia
Acanthaceae**	Agavaceae*	Araceae*
Arecaceae*	Balsaminaceae**	Convolvulaceae**
Bromeliaceae*	Commelinaceae*	Cucurbitaceae**
Costaceae*	Maranthaceae*	Cyperaceae*
Dioscoridaceae*	Piperaceae**	Gesneriaceae**
Euphorbiaceae**	Poaceae*	Primulaceae**
Heliconiaceae*	Rubiaceae*	Urticaceae**
Juncaceae*		Violaceae**
Malvaceae*		Zingiberaceae*
Smilacaceae*		
Solanaceae**		

The treeline is the ecological limit of herbaceous species richness with a decrease on richness near of this zone (Wesche *et al.* 2008). Herbs are more directly influenced by microclimatic environments than by macroclimatic limitations (Wang *et al.* 2009). Numerous monocot families, instead, have originated in the tropics and have had only restricted success in adjusting to low temperature, particularly frost (Márquez *et al.* 2006).

Herbs in tropical forests play a significant role in space antagonism for seedling and young trees due to light restriction (Zivanai *et al.* 2010), influencing in forest dynamics and tree regeneration (Condit *et al.* 2000). Also, herbaceous angiosperms are morphologically more flexible in their adaptations to low temperatures and have shorter generation periods than trees, which enables them to diversify more rapidly at higher latitudes (Willinghöfer *et al.* 2011). For all the previous reasons the species richness patterns of herbaceous angiosperms embody an extremely stimulating field of investigation that might supplement the wide investigation conducted particularly on trees. Given, the current high debate with regard to distributional patterns on herbaceous angiosperms, it is quite surprising that there are not general conclusions. Hence, this dissertation will contribute to filling the knowledge gap on this them.

1.4 Project framework and study area

The study was conducted at eight sites along an elevational gradient between 30 and 3540 m on the Eastern slopes of the Cofre de Perote, an extinct volcano of 4282 m elevation in the central part of the state of Veracruz, Mexico (Fig. 1.4). This region is located at the junction of the Trans-Mexican volcanic belt and the Sierra Madre Oriental, a mountainous area between 19° 25' 5.7" and 19° 36' 54" N and 94° 44' 43.5" and 97° 9' 36.9" W.

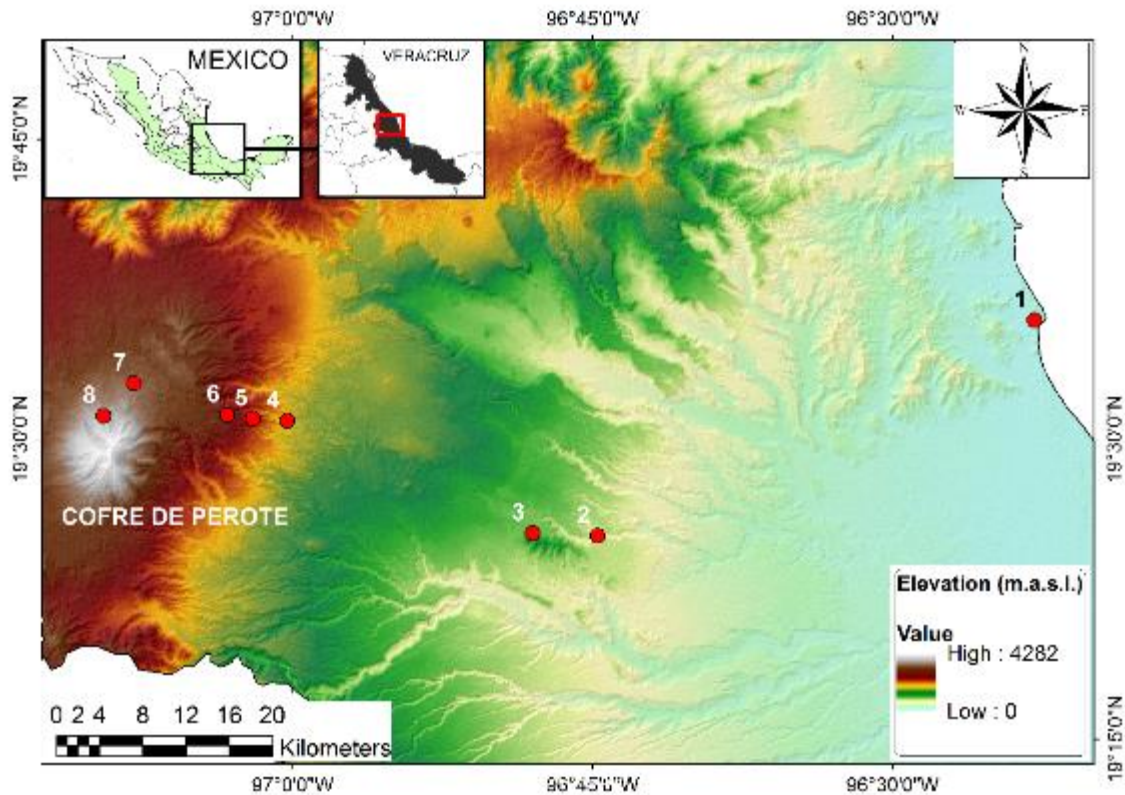


Figure 1.4 Location of the eight study sites along the elevational gradient on the Eastern slopes of the Cofre de Perote, the central part of the state of Veracruz, Mexico.

Due to its geomorphological conditions, the study area presents a high variation of climates, from warm at the lower part, over temperate at the mountainous mid-elevations to cold in the higher parts (Soto-Esparza & Giddings 2011). The temperature shows a linear decrease with elevation, whereas the mean precipitation varies depending on the elevation with a maximum at the mid-elevations and decreasing values at the extremes of the gradient (Fig. 1.5) (SMN 2016).

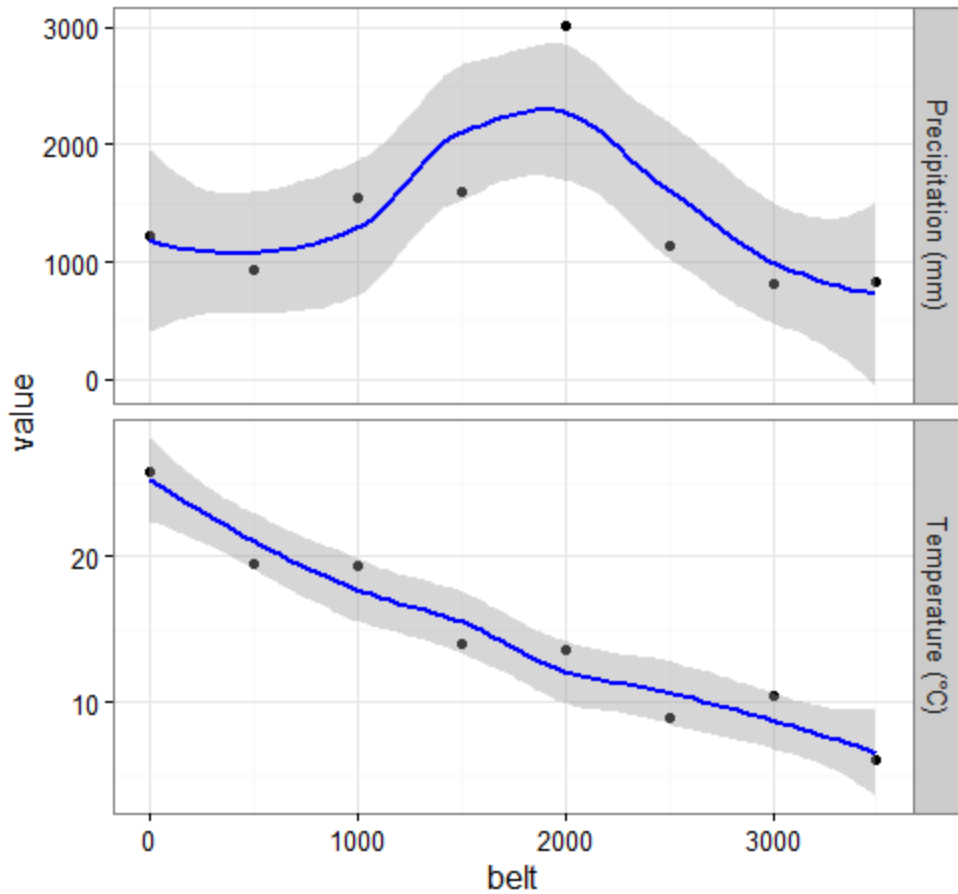


Figure 1.5 Mean annual precipitation and temperature measured in different climatological stations (near to the sampling sites) operating along the elevational gradient during the period 1951-2010 (SMN 2016).

The orographic and climatic differences along the transect allow the presence of different vegetation types, from the dry environments with high temperatures (tropical semi-deciduous forest and tropical oak) over the humid-temperate (humid montane forest, pine-oak forest) to cold and dry at the higher parts of the gradient (pine and fir forest) (Fig. 1.6). According to Lauer (1973), five climate zones can be found in the study area in combination with six vegetation types following Miranda & Hernández-Xolocotzi (1963). The different vegetation types are described below based on field observations and in accordance with the reported by Castillo-Campos (2011).

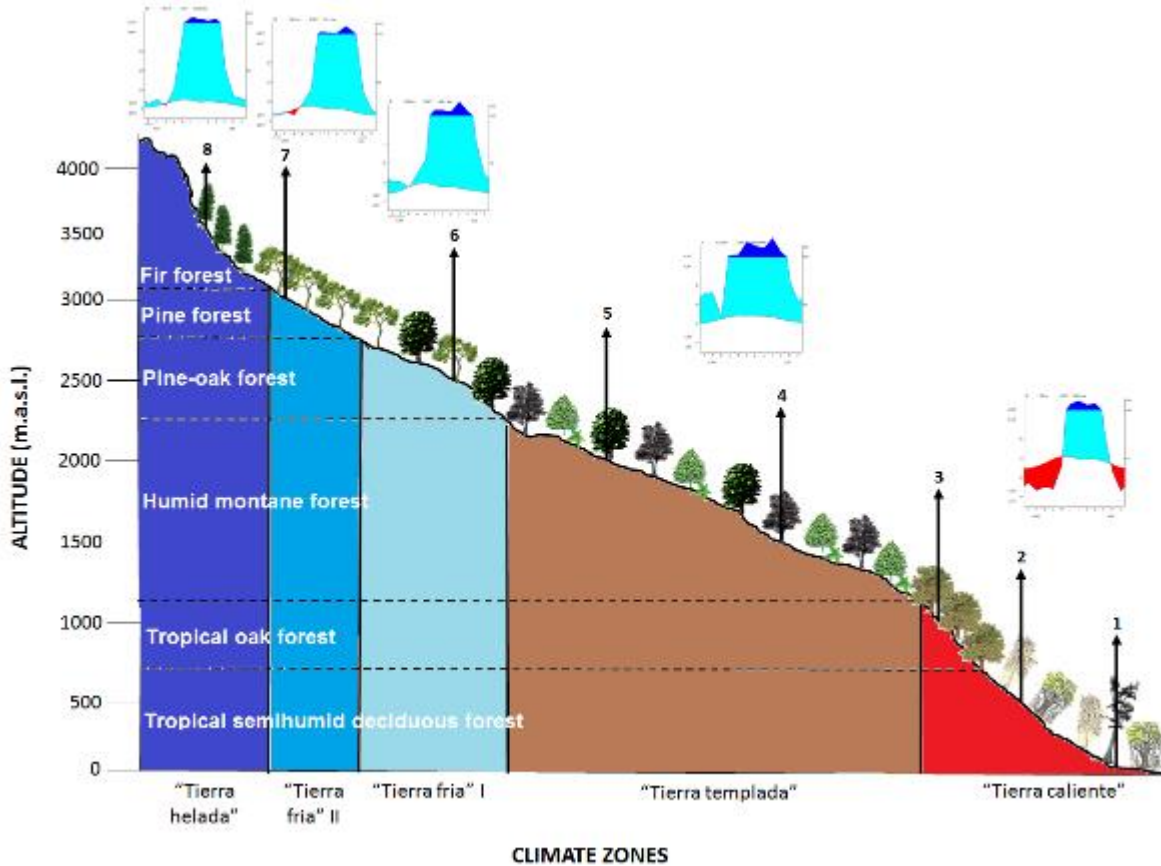


Figure 1.6 Different vegetation types according to Miranda & Hernández-Xolocotzi (1963) and climate zones (Lauer 1973) along the elevational gradient of the study area.

Tierra caliente (0-1250 m). In this zone, we selected three study sites located in two vegetation types: 1) tropical semi-humid deciduous forest that is found in the localities of La Mancha at 40 m and Palmarejo at 640 m (Fig. 1.7) (Castillo-Campos & Travieso-Bello 2006). The most important trees are *Bursera simaruba*, *Comocladia engleriana*, *Plumeria rubra* and some species of the genus *Quercus*. The shrub stratum is dominated by *Dioon edule*, *Chusquea* sp. and some species of *Chamaedorea*. The herbaceous stratum is dominated by some ferns of the genera *Adiantum* and *Tectaria*. The hemiepiphytes are represented by *Monstera* and *Philodendron* (Carvajal-Hernández 2016).

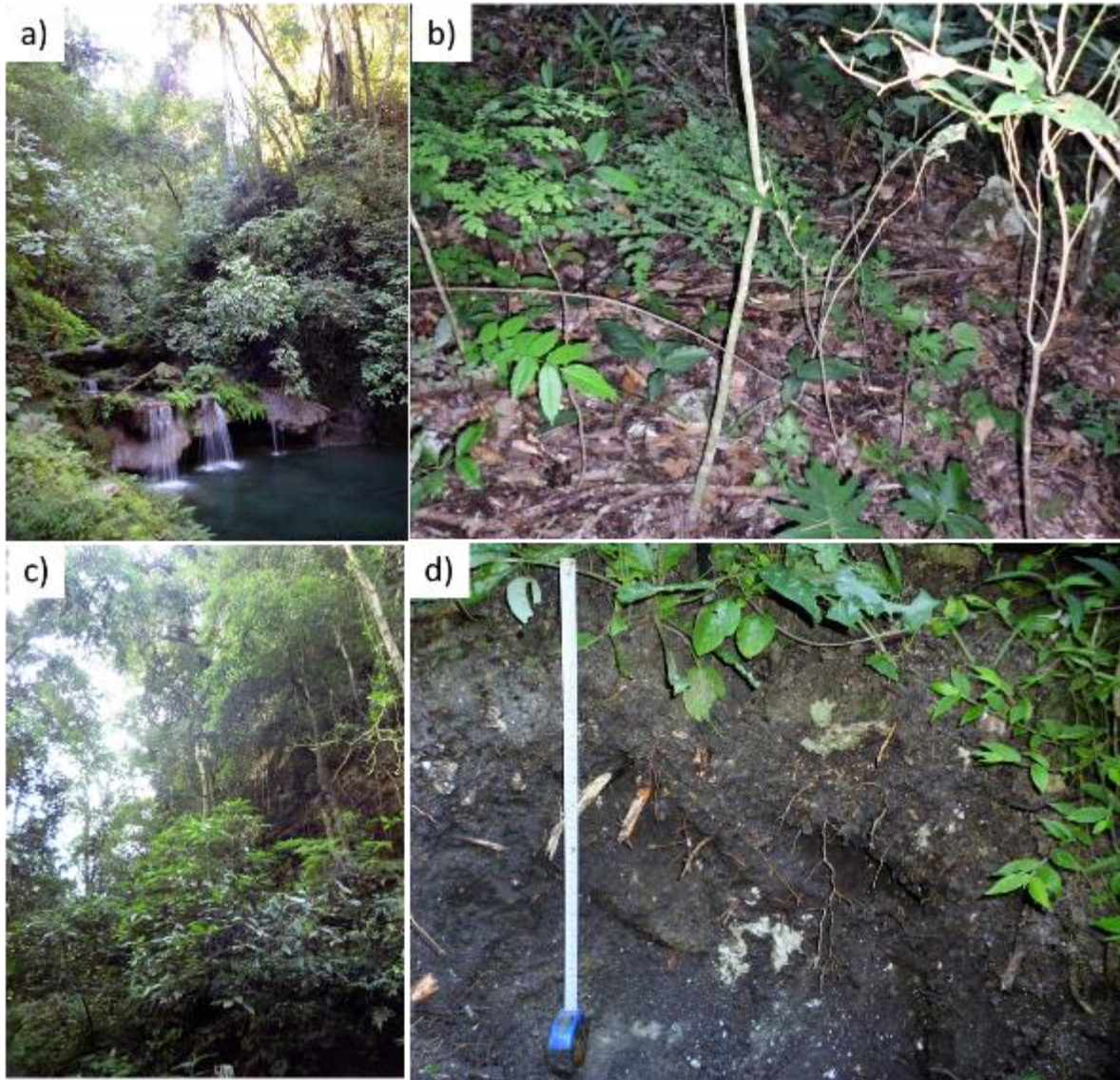


Figure 1.7 Tropical semi-deciduous forest: a) azonal riparian forest, b) herbaceous layer, c) vegetation structure and d) soil profile.

2) Tropical oak forest in the locality of Chavarrillo at 970 m (Fig. 1.8). This vegetation type is typically dominated by one to three oak species (*Quercus oleoides*, *Q. laurina*, *Q. sapotifolia*, *Q. peduncularis*), which do not exceed 15 m in height, whereas other tree species are scarce (*Byrsonia crassifolia*, *Pouteria campechiana*). In the shrub stratum grow *Acacia cornigera*, *A. pennatula* and *Malvaviscus arboreus*. In the herbaceous stratum stand out *Bromelia penguin* and *Blechnum occidentale* (Carvajal-Hernández

2016). Vascular epiphytes, such as xeromorphic bromeliads of the genus *Tillandsia* and orchids, are abundant (Torres-Cantú 2013).

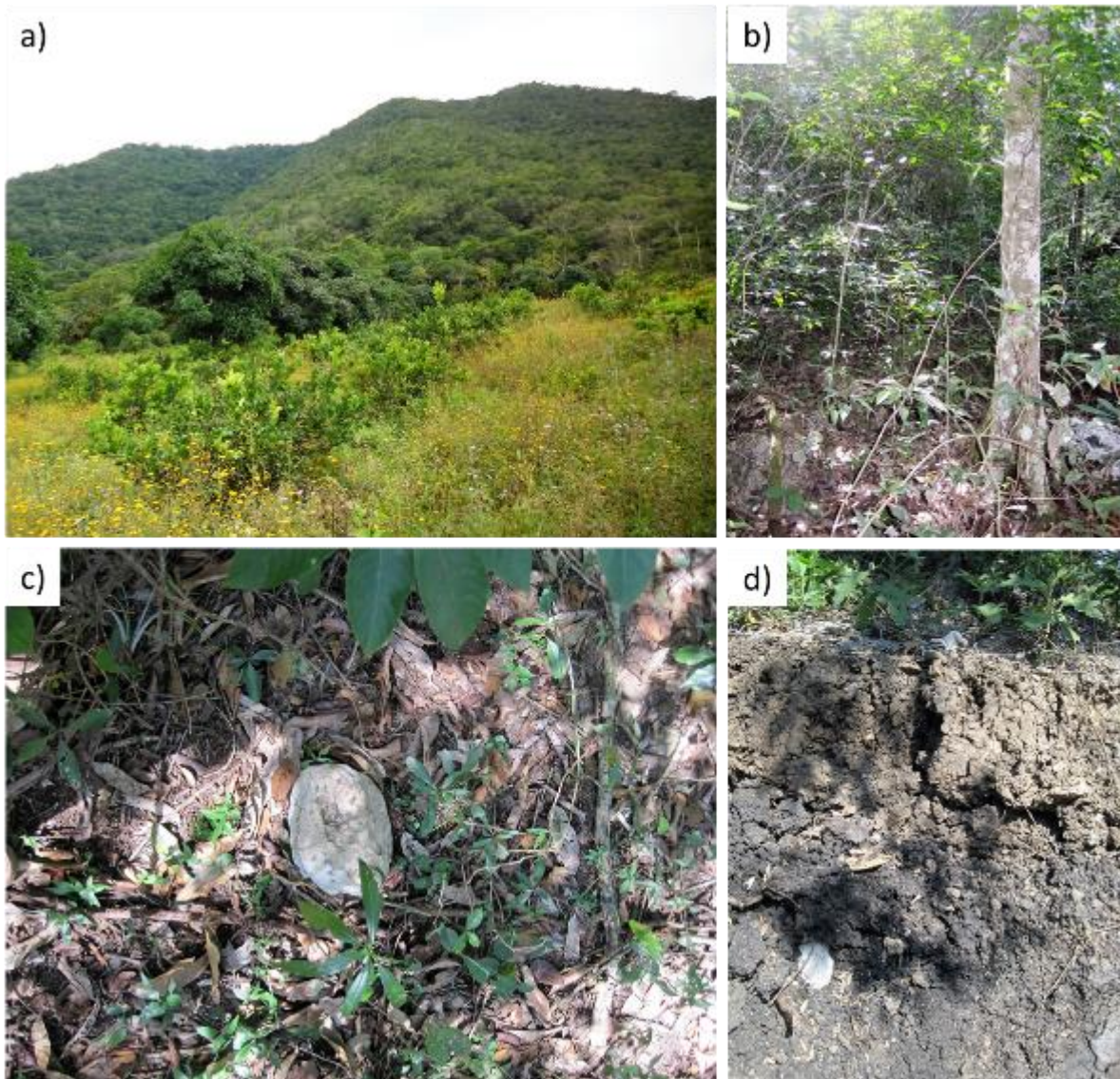


Figure 1.8 Tropical oak forest: a) landscape view of the study site, b) forest structure, c) herbaceous layer and d) soil profile.

Tierra templada (1250-2200 m). In this zone, two study sites within one vegetation type were chosen: 1) humid montane forest, which is found in the localities of Los Capulines

at 1570 m and El Zapotal at 2120 m (Fig. 1.9). One of the most important ecological factors that characterize this kind of forest is the frequency of fog (“bosque de niebla”; Zamora-Crescencio & Castillo-Campos 1997). In general, this community includes a mix of lower montane forest genera (*Quercus* spp., *Liquidambar* sp.) with tropical lowland forest families (Acanthaceae, Rubiaceae, Myrsinaceae). The most common shrubs are *Psychotria* sp. and tree ferns of the genera *Cyathea* and *Alsophila*. The epiphytic herbs stand out in this ecosystem, where the ferns are represented by several families and genera, as well as Bromeliaceae and Orchidaceae stand out for their high species richness and abundance (Carvajal-Hernández 2016). The period of foliar expiration is short and present in the dry cold season (November to March), although the forest is never fully defoliated (Zamora-Crescencio & Castillo-Campos 1997). There are numerous endemic (22 recorded for Veracruz), endangered and rare species reported in this vegetation (Gómez-Pompa & Castillo-Campos 2010).

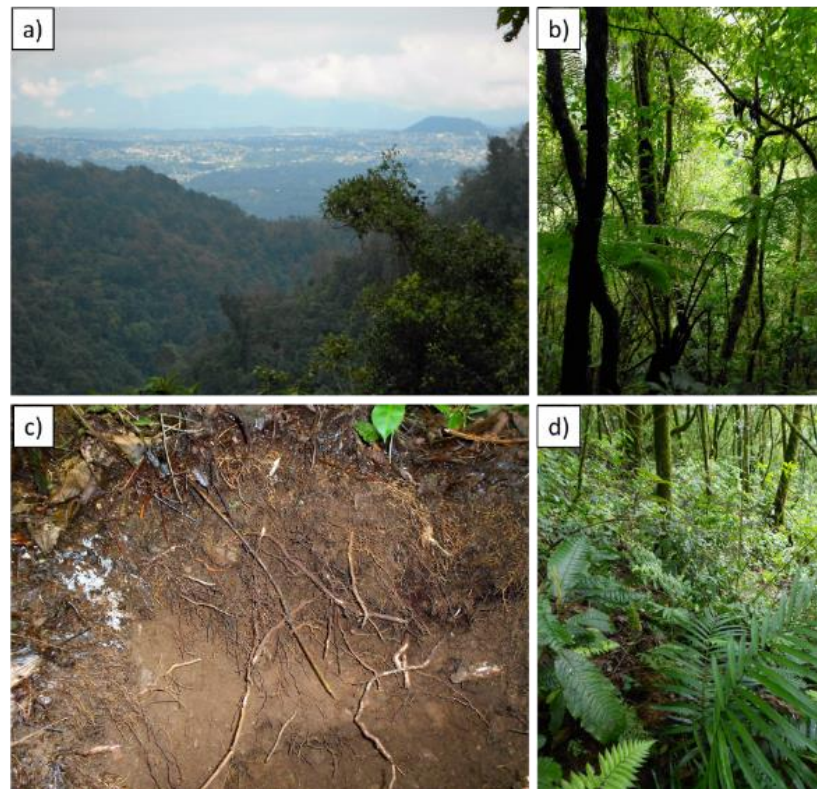


Figure 1.9 Humid montane forest: a) landscape view of the study site, b) forest structure, c) soil profile and d) herbaceous layer.

Tierra fría I (2200-2700 m). In this zone, one study site within one vegetation type was chosen, the pine-oak forest, which is found in the locality of El Encinal at 2520 m (Fig. 1.10). This vegetation type comprises a community whose dominant arboreal components belong to the genera *Quercus* (*Q. crassifolia* and *Q. laurina*) and *Pinus* and the shrub stratum is represented mainly by species of the genus *Senecio*. In the herbaceous stratum dominate species of the family Asteraceae, Poaceae, and ferns of different genera (Carvajal-Hernández 2016). Typically in the afternoons fog occurs, resulting in a high abundance of epiphytic mosses (Narave-Flores 1985, Castillo-Campos 2011).

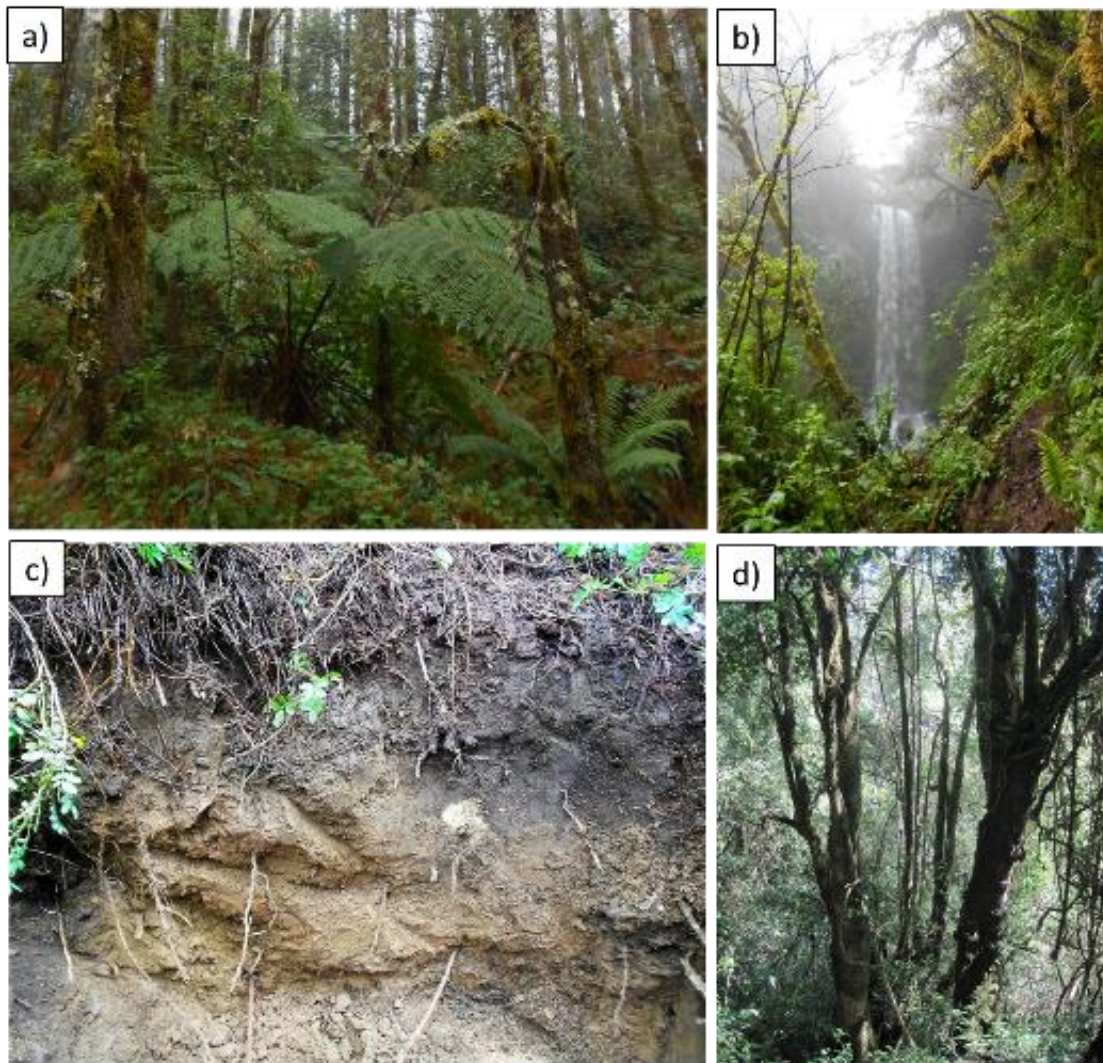


Figure 1.10 Pine-oak forest: a) herbaceous layer, b) azonal forest, c) soil profile and d) forest structure.

Tierra fría II (2700-3200 m). In this zone, one study site within one vegetation type was chosen, the pine forest, which is found in the locality of Los Pescados at 3110 m (Fig. 1.11). This vegetation type has a low plant richness, trees are dominated by several species of the genus *Pinus* (*P. montezumae*, *P. pseudostrobus*, *P. teocote*, and *P. patula*). The shrub stratum is composed by immature pines of the same species as the arboreal stratum and *Baccharis conferta*, and the herbaceous stratum is commonly dominated by grasses and species of the families Asteraceae, Crassulaceae mainly from the genus *Echeveria* and ferns of the genus *Dryopteris*. Vascular epiphytes are scarce, represented mostly by two species of ferns (*Pleopeltis polylepis*, *Polypodium plebeium*) (Carvajal-Hernández 2016). There are 12 endemic plant species for Veracruz in this forest type (Gómez-Pompa & Castillo-Campos 2010).



Figure 1.11 Pine forest: a) landscape view of the study site, b) forest structure, c) herbaceous layer and d) soil profile.

Tierra helada (3200-4282 m). In this zone, one study site within one vegetation type was chosen, the fir forest, which is found in the locality of El Conejo at 3520 m (Fig. 1.12). This vegetation type is a monospecific *Abies religiosa* community. These forests are confined to sites of high mountains, between 3,100 and 3,600 m. This plant community is composed of arboreal elements whose height varies between 20 and 40 m, the peculiar characteristic of its dominant elements is the typical triangular shape of its crowns. There are immature individuals of *A. religiosa* forming part of the shrubby and lower arboreal stratum, whereas the herbaceous stratum is dominated by many seedlings of the same species (Narave-Flores 1985).

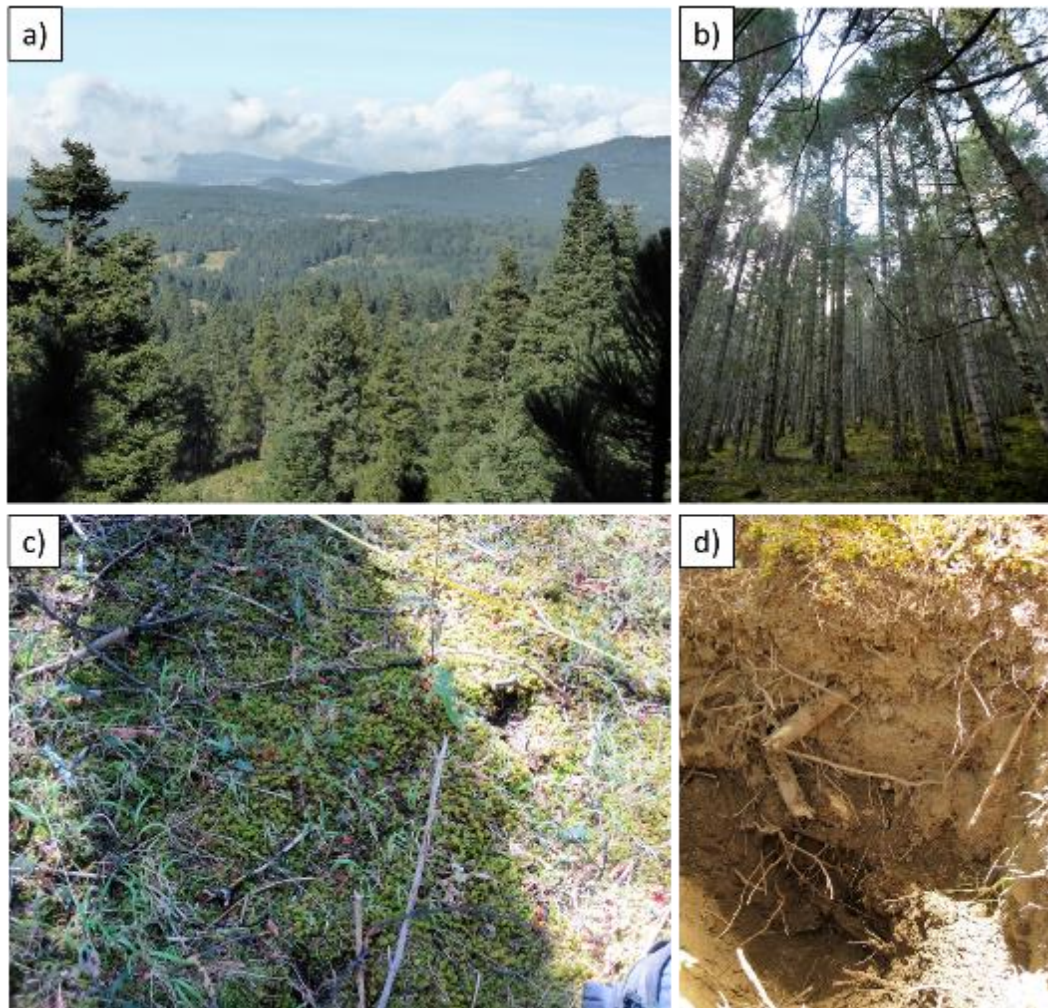


Figure 1.12 Fir forest: a) landscape view of the study site, b) forest structure, c) herbaceous layer and d) soil profile.

1.5 Study objectives and general study aim

Despite the investigations realized on elevational gradients and the effect of land use intensity on plant diversity, relevant research on herbaceous angiosperms is still scarce compared to other groups of vascular plants, such as trees. The study of an elevational gradient proposed in this work provides an opportunity to analyze distributional patterns of herbs in a tropical area with contrasting environmental conditions.

1.5.1 Research questions

- What are the patterns of diversity and distribution of herbaceous angiosperms along an elevational gradient in central Veracruz, Mexico, compared with those found in other Neotropical countries and tropical latitudes?
- What is the impact of forest use intensity on the diversity of herbaceous angiosperms?
- What is the current conservation status of forest fragments in central Veracruz, Mexico?

1.5.2 General hypothesis

The abiotic factors related to climatic parameters, such as temperature, solar radiation, and relative humidity, have an influence on the species distribution patterns. There is evidence that in presence of anthropogenic disturbance the microclimatic conditions change, which causes pressure on the species diversity. Consequently, it is expected that the present climatic conditions along the studied elevational gradient as well as its modification due to the human disturbance have an influence on the patterns of distribution and diversity of herbaceous angiosperms. Furthermore, it is hypothesized that the fragmentation and degradation of the forests in the study area have been increasing over time, which has also increased the pressure on the herb diversity. Therefore, it is expected that the current spatial distribution of herbs is due to a long history of land use in the study area.

1.5.3 Objectives

- To evaluate the patterns of distribution and diversity of herbaceous angiosperms along an elevational gradient (20 to 3500 m) in central Veracruz, Mexico.
- To evaluate the effect of land use intensity on the richness and composition patterns of herb species.
- To analyze the current conservation status of forest fragments in the study area.

1.6 Thesis structure

This thesis is divided into three studies concentrating on diverse features of floristics, distributional patterns, diversity and composition of herbaceous angiosperms in different elevations and degrees of land use intensity as well as land use change and forest fragmentation.

CHAPTER 2:

Richness and distribution of herbaceous angiosperms along gradients of elevation and forest disturbance in central Veracruz, Mexico.

In this chapter, the species richness and floristic composition of herbaceous angiosperms at eight elevational sites were compared with respect to forest use intensities. Furthermore, the role of environmental heterogeneity formed by old-growth, degraded and secondary forests as a reservoir of species richness of herbs was assessed.

The following hypotheses were tested:

1. Species richness of herbaceous angiosperms follows a hump-shaped pattern along the elevational gradient.
2. Species richness of herbaceous angiosperms decreases with land use intensity.

CHAPTER 3:

Diversity and composition of herbaceous angiosperms along gradients of elevation and forest use intensity.

In chapter 3 diversity patterns, as well as floristic composition in six vegetation belts at different elevations and in different habitats, were studied. We analyzed the influence of elevation and forest use intensity on alpha, beta, and gamma diversity.

The following hypotheses were tested:

1. Herb species richness on the plots (α -diversity) increases from old-growth to degraded and decreases in secondary forest.
2. A continuous turnover in species composition from old-growth over degraded to secondary forest.
3. β -diversity is the most important component of γ -diversity due to the forest heterogeneity.

CHAPTER 4:

Deforestation and forest fragmentation in central Veracruz, Mexico since the 1990s.

In this chapter, the deforestation and fragmentation patterns of the study area during three different periods (1993, 2000 and 2014) were examined. We obtained the land-cover classification of the study area, quantified the net change in forest area and the loss of original (gross) forest, and finally quantified and compared the spatial arrangement of native forest fragments, using landscape indexes. Finally, we presented further conclusions for forest conservation strategy in the region.

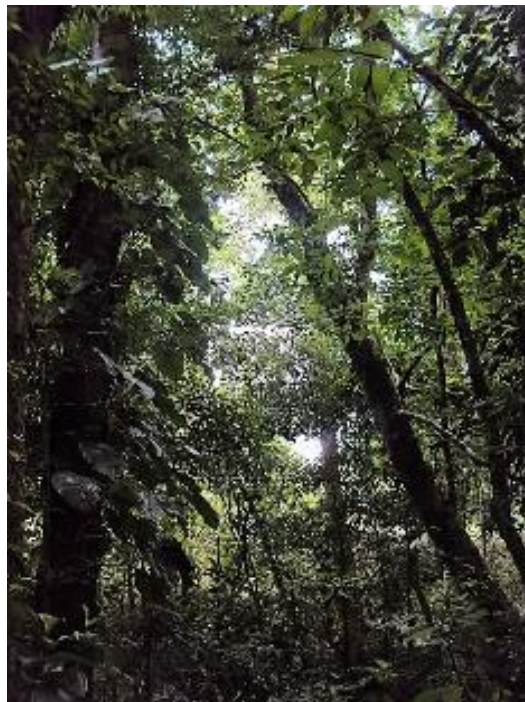
The following hypotheses were tested:

- There is a continuous deforestation in the study area since 1993.
- The current forest patches in the study area are highly isolated and fragmented.

CHAPTER 2: Richness and distribution of herbaceous angiosperms along gradients of elevation and forest disturbance in central Veracruz, Mexico

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Humid montane old-growth forest in *Los Capulines*, Veracruz, Mexico at 1500 m.

2 Richness and distribution of herbaceous angiosperms along gradients of elevation and forest disturbance in central Veracruz, Mexico

2.1 Abstract

Background: Terrestrial herbs are a significant floristic element of tropical forests; however, there is a lack of research focused on this plant group.

Question: Which are the patterns of species distribution of herbaceous angiosperms along gradients of elevation and forest disturbance at Cofre de Perote, central Veracruz, Mexico?

Studied species: Terrestrial herbaceous angiosperms.

Study site and years of study: Eastern slopes of Cofre de Perote, central Veracruz, Mexico; from 2012 until 2014.

Methods: We established an elevational transect (40 to 3,520 m), where we realized floristic sampling in eight study sites within elevational belts of about 500 m each. We recorded the occurrence of terrestrial angiosperm herbs within a total of 135 plots of 20 x 20 m, distributed in old-growth, degraded, secondary forest, as well as azonal vegetation. We analyzed species richness and floristic composition and then compared the resulting data between the different elevational belts and degrees of forest disturbance.

Results: We recorded a total of 264 herb species, 31 endemic to Mexico and three classified as threatened. The total number of species represents 5.7% of species of the Veracruz' herbaceous angiosperm flora. The elevational belts with highest species richness were 2,500 m (76) and 1,500 m (52). In most of the cases, secondary forests showed the highest species richness along the elevational gradient, whereas old-growth forests had fewer species.

Conclusions: The observed species richness, including endemic elements, highlights the importance for plant conservation of the area which is threatened by land use changes.

In addition, we suggest that environmental heterogeneity formed by mature, disturbed and secondary forests is acceptable (and unavoidable) and can even increase species richness.

2.2 Introduction

Growing human pressure on terrestrial ecosystems represents one of the most important threats to biodiversity, especially in the tropics (Godfray *et al.* 2010, Melo *et al.* 2013, FAO 2014b). Therefore, the planet is suffering rapid and dramatic changes across the majority of biomes (Foley *et al.* 2005). Considering the current high rates of deforestation in most of the tropical countries (Lindenmayer *et al.* 2006), it is projected that areas with old-growth forests will become increasingly scarce and fragmented (Köster *et al.* 2009, FAO 2014b). Human population growth and the intensification of agricultural practice are the major factors that threaten old-growth forests and their associated biodiversity in the tropics (Wright 2005), due to their conversion into cropland, grassland for cattle and human settlements (Foley *et al.* 2005). Consequently, complete floristic inventories documenting which species are affected by human interference are urgently needed (DeClerck *et al.* 2010).

The Mesoamerican region including Mexico is considered as a hotspot of plant diversity, meaning that it is very rich in endemic species, but also highly threatened (Myers *et al.* 2000). The main reason is the loss of primary vegetation due to high deforestation and urbanization rates (Wright & Muller-Landau 2006). Within Mexico, the state of Veracruz is considered a priority site for national and global conservation of biodiversity due to its outstanding geographical characteristics, such as the complex topography and the transition between tropical and temperate zones (Olguín 2011). Veracruz covers an area of 72,420 km² of which less than 20% consists of natural vegetation, with a high degree of habitat fragmentation (Gómez-Pompa *et al.* 2010, CONABIO 2011). Nevertheless, Veracruz hosts a large number of angiosperms (6,876 species) that represents about 31% of the flora of Mexico (Villaseñor & Ortíz 2012), and thus it is considered as the country's third richest state in angiosperms after Oaxaca and Chiapas (Rzedowski 1993, Villaseñor & Ortíz 2014). The state is also known for having all vegetation types registered in Mexico

(Gómez-Pompa & Castillo-Campos, 2010), according to the classification of Rzedowski (2006). Despite being a region with high species richness, there are still many parts of the state which lack a reliable floristic inventory (Gómez-Pompa *et al.* 2010), especially in remote montane areas, such as our study area. Until now, no floristic investigation along this elevational gradient was conducted, taking into account terrestrial herbaceous angiosperms, human land use intensity and geoecological conditions.

In the last two decades studies about diversity patterns of tropical vegetation along elevational gradients have received substantial consideration (Vázquez & Givnish 1998, Colwell *et al.* 2008, Willinghöfer *et al.* 2011), but the focus considering different taxonomical plant groups is unevenly distributed because most of the research is concentrated in the most species-rich herbaceous family (e.g., Poaceae, Asteraceae, Araceae) of every study area (Willinghöfer *et al.* 2011). However, many other herbaceous angiosperm families, such as Orchidaceae, Zingiberaceae, and Begoniaceae, are significant elements in the composition of tropical vegetation (Willinghöfer *et al.* 2011, Cicuzza *et al.* 2013). Moreover, terrestrial herbs play an important role in various ecological processes, such as tree regeneration and forest dynamics (Grubb 1977).

Nevertheless, terrestrial forest herbs have been little studied from a floristic and biogeographic point of view. As a result, there is little knowledge about how herbaceous angiosperm associations change along elevational gradients, and if they exhibit similar patterns like other plant groups (Willinghöfer *et al.* 2011). Only a few relevant studies were realized in pasture (Guevara & Laborde 2007) and coffee plantations (Ramos *et al.* 1983) or focusing on single families, such as Poaceae (Hernández *et al.* 1990, Mejía-Saulés *et al.* 2002), Orchidaceae (Sosa & Platas 1998, Salazar 1999) and Asteraceae (Villaseñor *et al.* 2006). Besides, the lack of specialists and taxonomic literature in different groups of these plants, as well as the seasonality of herb phenology, are important constraints for floristic studies because in lists some representatives of this biotype are omitted.

Further studies on the geographical distribution of the floristic elements of central Veracruz are necessary in order to better understand its complex mix of plant species (Villaseñor 2010). Inventories of specific groups of plants or particular geographic areas contribute to the completion of the national flora of Mexico and form the basis for the

appropriate management of the natural resources (Martinez-Camilo *et al.* 2012). This kind of data can also provide information about the degree of endemism and endangered species in specific areas, which allows evaluating protected areas about the richness and uniqueness of their flora (Rzedowski 2006).

The objective of this study was to record the flora of herbaceous angiosperms in central Veracruz, Mexico, along gradients of elevation and human forest use intensity at the slopes of the *Cofre de Perote* mountain. The study was conducted to gather information about the floristic composition, elevational ranges and geographical distribution of the species, as well as to compare species richness and similarity between elevational belts and forest types. In this way, we provide more detailed information about patterns of species richness and distribution, which presents another step towards defining priority areas for conservation of this complex vegetation mosaic.

2.3 Materials and methods

2.3.1 Study area

The study was conducted at eight study sites along an elevational gradient of ca. 82 km between 40 and 3,520 m.a.s.l. on the eastern slopes of the *Cofre de Perote*, an extinct volcano of 4,282 m elevation in the central part of the state of Veracruz, Mexico (Fig. 2.1). This region is located at the junction of the Trans-Mexican volcanic belt and the *Sierra Madre Oriental*, a mountainous area between 19° 25' 5.7" and 19° 36' 54" N, and 96° 22' 36" and 97° 09' 36.9" W. According to Lauer (1972), five climate zones can be found in the study area in combination with six forest types as classified by Miranda & Hernández-Xolocotzi (1963) (Table 2.1).

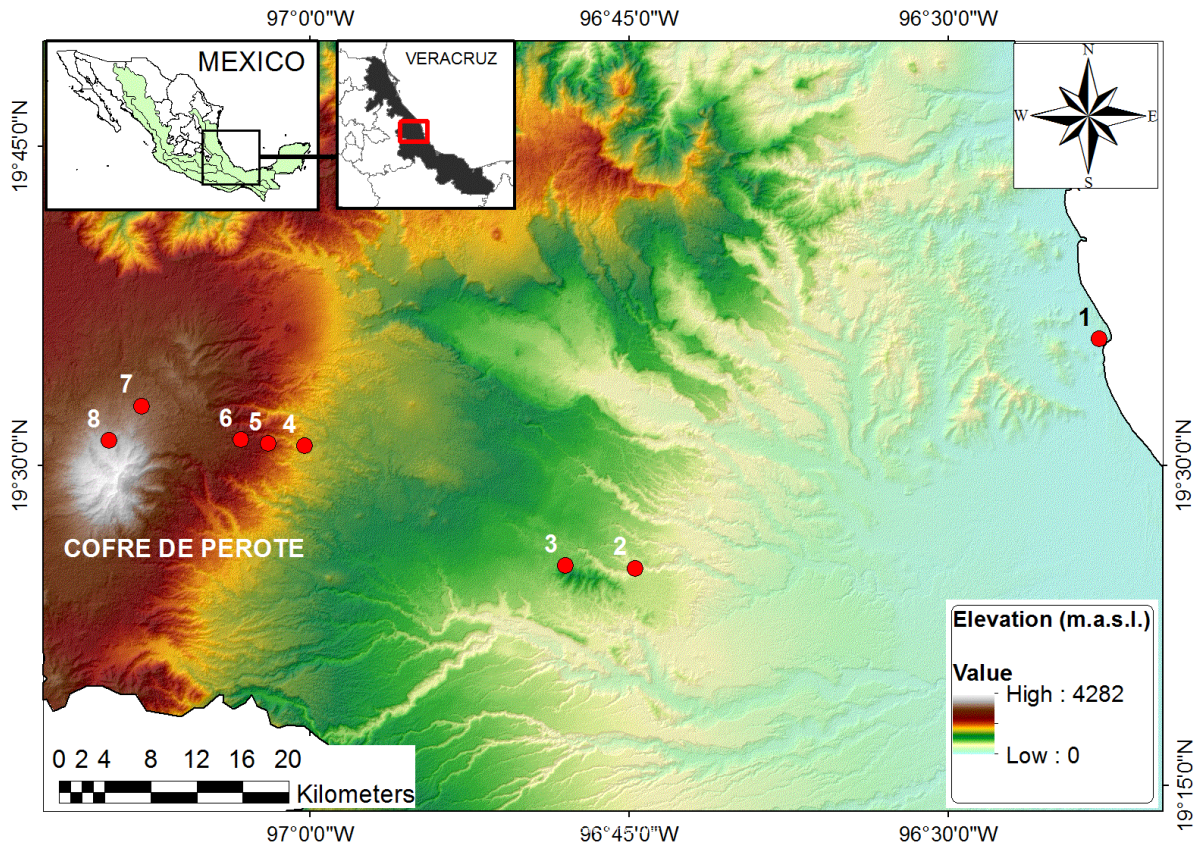


Figure 2.1 Location of the eight study sites along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico. Study locations: 1. La Mancha (50 m); 2. Palmarejo (650 m); 3. Chavarrillo (1,000 m); 4. Los Capulines (1,600 m); 5. El Zapotal (2,100 m); 6. El Encinal (2,500 m); 7. Los Pescados (3,100 m); 8. El Conejo (3,500 m). The limits of the Neotropics according to Löwenberg-Neto (2014) are shown in light green.

Table 2.1 Overview of the study sites along the elevational gradient at Cofre de Perote, central Veracruz, Mexico, with information on elevational range, forest type (TSDF= tropical semi-humid deciduous forest, TOF= tropical oak forest, HMF= humid montane forest, POF= pine-oak forest, PF= pine forest, and FF= fir forest), annual temperature annual precipitation and number of recorded species within the four habitats with different forest use intensities (OG= old-growth, DE= degraded, SE= secondary, AZ= azonal).

Study site	Elevational range (m)	Forest type	Number of plots	Temp. (°C)	Prec. (mm)	OG	DE	SE	AZ
<i>La Mancha</i>	30-50	TSDF	15	26	1,221	4	6	8	-
<i>Palmarejo</i>	610-670	TSDF	20	23	938	12	35	11	20
<i>Chavarrillo</i>	900-1,010	TOF	15	21	1,552	11	13	19	-
<i>Los Capulines</i>	1,470-1,650	HMF	20	18	1,598	24	21	20	31
<i>El Zapotal</i>	2,020-2,230	HMF	15	14	3,004	16	18	20	-
<i>El Encinal</i>	2,470-2,600	POF	20	12	1,142	47	41	38	35
<i>Los Pescados</i>	3,070-3,160	PF	15	10	821	22	26	37	-
<i>El Conejo</i>	3,480-3,540	FF	15	8	829	9	13	10	-

Tierra caliente (0-1,250 m).- In this climate zone, we selected three study sites located in two forest types (Fig. 2.1, Table 2.1): the tropical semi-humid deciduous forest (TSDF) is found in the localities of *La Mancha* at 50 m and *Palmarejo* at 650 m (Castillo-Campos & Travieso-Bello 2006) and characterized by the trees *Brosimum alicastrum*, *Cedrela odorata*, *Bursera simaruba* and *Ficus obtusifolia*. Canopy trees lose leaves mostly during the prolonged period of drought (October to May). The tropical oak forest (TOF) in the locality of *Chavarrillo* at 1,000 m is typically dominated by one to three oak species (*Quercus oleoides*, *Q. laurina* and/or *Q. peduncularis*), whereas other tree species are

scarce. The period of leaf fall lasts about four months and it is related with the dry season (February to May).

Tierra templada (1,250-2,200 m).- In this climate zone, two study sites within one forest type were chosen (Fig. 2.1, Table 2.1): the humid montane forest (HMF), which is found in the localities of *Los Capulines* at 1,500 m and *El Zapotal* at 2,100 m. One of the most important ecological factors that characterize this kind of forest is the frequent occurrence of fog (*bosque de niebla* or *cloud forests*; Zamora-Crescencio & Castillo-Campos 1997). In general, this community includes a mix of lower montane forest genera (e.g., *Quercus* and *Liquidambar*) with tropical lowland forest families (Acanthaceae, Rubiaceae, and Myrsinaceae). The period of leaf fall lasts about four months and is related to the dry season (February to May).

Tierra fría I (2,200-2,700 m). - In this climate zone, one study site within one forest type was chosen (Fig. 2.1, Table 2.1): the pine-oak forest (POF), which is found in the locality of *El Encinal* at 2,500 m. This forest type comprises a community whose dominant trees belong to the genera *Quercus* and *Pinus*. Typically, in the afternoons fog occurs (Narave-Flores 1985, Castillo-Campos 2011), which makes that the temperature and humidity stay constant.

Tierra fría II (2,700-3,200 m).- In this climate zone, one study site within one forest type was chosen (Fig. 2.1, Table 2.1): the pine forest (PF), which is found in the locality of *Los Pescados* at 3,100 m. This forest type is dominated by several species of the genus *Pinus* (*P. montezumae*, *P. patula*, *P. pseudostrobus*, *P. teocote*) causing a high canopy openness.

Tierra helada (3,200-4,282 m). - In this climate zone, one study site within one forest type was chosen (Fig. 2.1, Table 2.1): the fir forest (FF), which is found in the locality of *El Conejo* at 3,500 m. This forest type is a monospecific *Abies religiosa* community with sparse canopy openness.

Along the complete elevational gradient, mean annual precipitation (MAP) ranges from 813 to 3,004 mm, being highest in the humid montane forest at 2,100 m and lowest in coniferous forests above 3,000 m, whereas mean average temperature (MAT) ranges

from 9 to 26°C (SMN 2016) (Table 2.1). The elevational vertical temperature gradient follows a negative linear pattern with MAT decreasing by 0.55°C every 100 m ($r^2= 0.96$, $p < 0.001$).

2.3.2 Sampling and botanical records

Field sampling was conducted between February 2012 and January 2014 at eight sites within elevational belts of about 500 m each (Fig. 2.1, Table 2.1). In order to simplify hereafter we will refer to every site as categorical unit (50, 650, 1,000, 1,500, 2,100, 2,500, 3,100, 3,500 m).

We studied terrestrial herbaceous angiosperms (excluding epiphytes), whose life form was defined as plants that have no persistent woody stem above ground or plants that are only slightly woody, rooted on the forest floor and have a short height (Moreno 1984, Poulsen 1996). Ferns were not included in this study because their diversity patterns were already described in the work of Carvajal-Hernández & Krömer (2015). Presence-absence was recorded for all species in each elevational belt within 15 to 20 plots of 20 × 20 m. The plot size of 400 m² was selected in order to have a representative study area of the forest fragments, which is small enough to keep abiotic factors and ecological physiognomy uniform within the plot (Kessler & Bach 1999). The total number of plots for the entire study was 135, resulting in a total study area of 54,000 m². For our study, we defined four types of habitat with different forest use intensities following Newbold *et al.* (2015): old-growth, degraded, secondary and azonal forest (Table 2.2).

Table 2.2 Classification of habitats with different forest use intensities according to the main physiognomic characteristic, the gap fraction in the canopy, dominance of canopy trees, percentage of shrubs and the presence of lianas (Newbold *et al.* 2015).

Habitat	Characteristic	Gaps (%)	Forest use intensity	Canopy trees	Shrub (%)	Lianas
Old-growth	No obvious forest use, dominance of mature trees	<10	Low	High	<30	No
Degraded	Selective logging, grazing and understory removal	11-25	Medium	Low	30-50	Low
Secondary	regrown after clear-cut	>25	High	Very low	>50	High
Azonal	Grows in riparian forest and humid ravines	<10	Low	High	<30	No

To avoid edge effects, our plots were established at least 50 m away from the nearest forest edge. An equal number of plots was studied for every forest type, i.e. five were established in each of the following habitats with different use intensities: i) old-growth, ii) degraded and iii) secondary forest. Only in the sites of 650 m, 1,500 m and 2,500 m we were able to add five plots in vi) existing azonal vegetation, causing the uneven numbers of plots per elevational belt (Table 2.1).

2.3.3 Taxonomic determination

In each study site (but not in every plot), all terrestrial herbaceous angiosperms species were collected mostly in triplicate and deposited at the following herbaria: *Herbario Nacional de México, Instituto de Biología, UNAM, (MEXU, including all unicates), Instituto de Ecología, A.C., (XAL), Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, IPN (CIIDIR)* and/or at the local herbarium of the *Facultad de Biología, Universidad Veracruzana (XALU)*. Collection and processing of botanical specimens were made according to the proposal of Lot & Chiang-Cabrera (1986). Botanical determinations

were realized by use of the relevant taxonomic literature (*Flora de Veracruz* and *Flora fanerogámica del Valle de México*), by comparison with specimens deposited at MEXU and XAL, and consultation of experts in different plant families (see Acknowledgements). Also, morphospecies which are clearly different were incorporated in the floristic list (Krömer *et al.* 2013). It was not possible to identify all specimens to species or genus level for two main reasons: i) most of the studied plant groups are not well known and their identification is difficult due to a lack of relevant literature, ii) some individuals were found sterile. Taxa were classified according to the classification of the Angiosperm Phylogeny Group (APG) (Bremer *et al.* 2009).

2.3.4 Data analyses

We used the package “vegan 2.3-4” (Oksanen *et al.* 2016) in R software 3.2.3 (R Core Team 2014) to calculate the number of unobserved species with the Bootstrap function, which is based on presence-absence data and takes into account rare, unique and duplicated species. This species richness estimator is reliable because it has a sensibility to species aggregation in the initial stage of the sampling when the species distribution is random.

Based on their geographical distribution area, each species was placed in one of the following categories (*sensu* Rzedowski 1991): i) endemic to Mexico, ii) endemic to the southern United States and Mexico (Megamexico 1), iii) endemic to Mexico and Central America (Megamexico 2), iv) endemic to the southern United States and Central America (Megamexico 3), and v) introduced species (Gómez-Pompa *et al.* 2010, Espejo-Serna 2012).

Finally, to compare our results with other studies, we calculated the taxonomic diversity index (TDI) (Magurran 2004) for the total number of species and for the three most important families: Asteraceae, Poaceae, and Orchidaceae, with the following equation:

$$TDI = \frac{\log S}{\log A}$$

where S is the total species number and A is the entire studied area in m^2 .

2.4 Results

In 135 plots along the elevational transect, we recorded 264 (morpho-) species of terrestrial herbaceous angiosperms from 152 genera and 54 families (Appendix). Of all recorded species, 201 (76%) were identified to species level, 42 (16%) to genus level and 21 (8%) to family level. Monocots contributed 45% of the species and 28% of the families, and dicots 55% of the species and 72% of the families. Table 2.3 summarizes the most species-rich taxa at family and genus level. The observed species richness varied between 79 and 90% of the predicted values by the estimator Bootstrap at every elevational belt (Fig. 2.2).

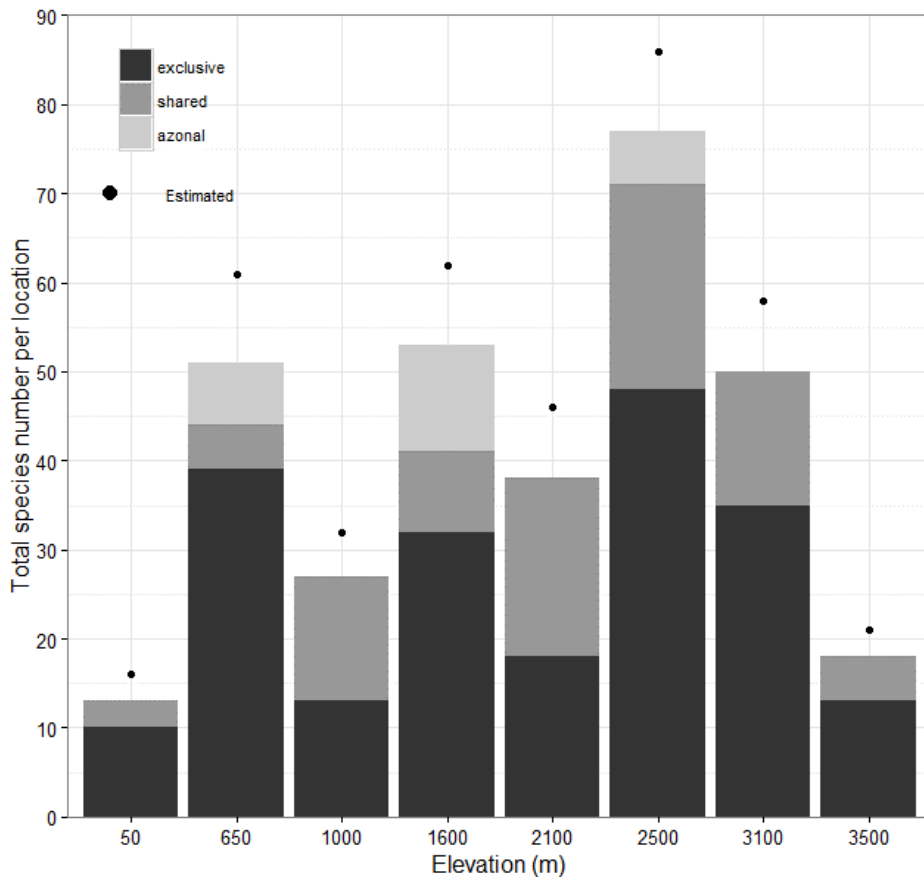


Figure 2.2 Observed and estimated (Bootstrap species richness estimator) species richness of all species together per elevational belt. It is shown the number of exclusive species at each study site, the number of species shared with other sites, and the species that are exclusive for azonal habitats.

Table 2.3 Most representative families and genera of herbaceous angiosperms along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico.

Family	Species number	%	Genus	Species number	%
Poaceae	36	14%	<i>Peperomia</i>	10	4%
Asteraceae	31	12%	<i>Salvia</i>	8	3%
Orchidaceae	27	10%	<i>Begonia</i>	6	2%
Cyperaceae	17	6%	<i>Senecio</i>	6	2%
Lamiaceae	13	5%	<i>Cyperus</i>	5	2%
Araceae	12	4%	<i>Anthurium</i>	5	2%
Piperaceae	10	4%	<i>Carex</i>	5	2%
Commelinaceae	9	3%	<i>Ageratina</i>	4	2%
Rubiaceae	8	3%	<i>Arenaria</i>	4	2%
Other families	101	38%	Other genera	211	80%
Total	264	100%	Total	264	100%

In order to compare overall species richness between the eight study sites, we used the values excluding and including species of azonal vegetation. In the first case, the highest number of species was found on the site of 2,500 (71), followed by 3,100 m (48) and 650 m (43); in the second case, the site with the highest number of species was 2,500 m (76), followed by 1,600 m (52) and 3,100 m (48) (Fig. 2.2). All habitats of the 2,500 m site taken separately had the highest species richness of the elevational gradient (Table 2.1), whereas all habitats of 50 m had the lowest richness. The secondary forest in most of the sites had the highest number of species, whereas old-growth forests had the lowest number of species in most of the sites. In the sites with azonal vegetation, this habitat had more species than old-growth forests, and except for 2,500 m, even more than secondary forests (Table 2.1). TDI was 0.51 for all species and between 0.31 and 0.033 for the three most important families (Table 2.4).

Table 2.4 Species richness of herbaceous angiosperms recorded in elevational gradient studies realized in Mexico and two different regions of the Neotropics, indicating its elevational range, latitude, area, TDI = taxonomic diversity index (calculated for the total species number and for the most important families Ast= Asteraceae, Poa= Poaceae and Orc= Orchidaceae).

Region, Country	Elevation (m)	Latitude	Species number	Area (ha)	TDI	Ast	TDI	Poa	TDI	Orc	TDI	Authors
Manaus, Brazil	70-150	2° 37' S	24	0.09	0.47	0	-	2	0.10	0	-	Costa (2004)
Cuyabeno, Ecuador	250-300	0° 00' S	70	1.00	0.46	0	-	8	0.23	0	-	Poulsen <i>et al.</i> (2006)
Los Tuxtlas, Veracruz, Mexico	140-1,670	18° 43' N	50	2.96	0.38	0	-	0	-	17	0.28	Krömer <i>et al.</i> (2013)
Jalcomulco, Veracruz, Mexico	350-900	19° 21' N	60	0.67	0.46	2	0.08	4	0.16	2	0.08	Palacios-Wassenaar <i>et al.</i> (2014)
Central Mexico Veracruz,	1,800-2,000	19° 29' N	139	0.02	0.92	2	0.13	4	0.26	2	0.13	García-Franco <i>et al.</i> (2008)
Sierra de Manantlán, Jalisco, Mexico	1,500-2,500	19° 30' N	181	4.30	0.49	ND	ND	ND	ND	ND	ND	Vázquez & Givnish (1998)
Central Mexico Veracruz,	50-3,500	19° 31' N	264	4.80	0.52	31	0.32	36	0.33	27	0.31	This study
Central Mexico Veracruz,	400-900	19° 37' N	300	1.20	0.61	42	0.40	53	0.42	2	0.07	Castillo-Campos (2007)
Pacific coast of Mexico	400-2,860	19° 45'	1,793	140,000	0.36	333	0.28	221	0.26	181	0.25	Vázquez <i>et al.</i> (1995)
Sierra de Zapalinamé, Coahuila, Mexico	1,590-3,140	25° 25' N	171	3.30	0.49	61	0.40	27	0.32	0	-	Encina-Dominguez <i>et al.</i> (2007)

2.4.1 Geographical distribution

Most of the study sites shared only low numbers of species (Fig. 2.2). The highest number of exclusive species was found at 2,500 m, followed by 650 m and 3,100 m. Concerning biogeography, 70% of the taxa showed a Neotropical affinity and we recorded 31 species endemic to Mexico, including two species (*Begonia multistaminea* and *Sedum obcordatum*) endemic to Veracruz (see Appendix). Furthermore, 20 species were endemic to Mexico and Central America and two to the South of United States of America and Mexico. Three species are listed in Official Mexican Law (SEMARNAT 2010), two of these are threatened and endemic to Mexico (*Anthurium podophyllum* and *Peperomia subblanda*), and another was under special protection (*Monotropa hypopitys*). Additionally, we found 14 introduced species to Mexico that were mostly recorded in secondary and degraded forests (Table 2.5 and Appendix).

Table 2.5 Geographic distribution and life strategy of species found along the elevational gradient at Cofre de Perote, central Veracruz, Mexico, in old-growth habitats and habitats derived from human forest use intensity. OG= old-growth forest, DE= degraded forest, SE= secondary forest, AZ= azonal forest. Total numbers of species in each category are also shown.

Category	OG	DE	SE	AZ	Total
Under special protection	1	2	2	-	3
Endemic to Veracruz	1	-	-	-	1
Endemic to Mexico	11	15	20	9	31
South of United States of America and Mexico	1	2	1	-	2
Mexico and Central America	9	12	11	9	20
Introduced	5	6	9	2	14
Ruderal	13	19	27	11	41
Generalist	65	92	73	56	152

2.5 Discussion

2.5.1 General taxa richness

A comparison with previous studies on terrestrial angiosperms and other plant groups in the state of Veracruz shows that we recorded a high number of species in our study. Although our sampling area was limited (5.4 ha), the total number of species recorded was higher than those reported by Cházaro-Basáñez (1992) who focused on a floristic description of the different forest types within the upper part of the same elevational gradient. Cházaro-Basáñez reported only 12 herbs in the humid montane forest, 17 in the pine-oak forest, two in the pine forest and 14 in the fir forest. Carvajal-Hernández & Krömer (2015) found 155 species of ferns and lycophytes in the same plots of our elevational gradient of which 82 were terrestrial species. Several studies from central Veracruz reported a lower number of terrestrial herbs, e.g., Palacios-Wasenaar *et al.* (2014) recorded 230 species of vascular plants of which 60 (26%) were herbs (Table 2.5). García-Franco *et al.* (2008) found 258 vascular plant species in similar forests, of which 139 (54%) were herbs. Novelo-Retana (1978) recorded 238 species of vascular plants of which 67 (28%) were herbs. Zamora & Castillo-Campos (1997) recorded 390 species of vascular plants of which 225 (58%) were herbs. The relatively high number of herb species might be explained by the large environmental gradient covered in our study and will be discussed in the next paragraphs.

In contrast, a higher number of herbaceous species has been reported in some studies from central Veracruz, e.g., Castillo-Campos *et al.* (2007) recorded 580 species of vascular plants of which 369 (64%) were herbs, and Narave-Flores (1985) recorded 853 species of vascular plants of which 557 (65%) were herbs. For Southern Veracruz, Ibarra & Sinaca (1987) recorded 991 species of vascular plants of which 536 (54%) were herbs. However, all these studies were realized in much bigger sampling areas than the present study.

Due to the limited number of similar transect studies in the study area we were only able to compare our results with the following studies realized in Southern Veracruz by Krömer *et al.* (2013), which however included mainly terrestrial ferns and only a few orchids and bromeliads, Western Mexico (Jalisco) by Vázquez & Givnish (1998) and Vázquez *et al.*

(1995), and Northern Mexico (Coahuila) by Encina-Domínguez *et al.* (2007). Furthermore, we compared our results with the species numbers of terrestrial angiosperms found along two elevational gradients of Brazil and Ecuador (Table 2.4).

In most of the cases, our study site shows a higher number of species than the other locations. The TDI also shows that excluding the works from central Veracruz, our study has a higher species per area value than the other studies (Table 2.4). These differences among the geographical areas can be explained by environmental factors, such as latitudinal influence, precipitation, temperature, elevation and soil nutrients (Vázquez & Givnish 1998, Cicuzza *et al.* 2013). The TDI indicates different patterns for the three most important families, e.g., there is an increase of the values of Asteraceae with elevation (Table 2.4), which is different from the family pattern shown in Mexico (Villaseñor *et al.* 2005). In the case of the Poaceae, the index shows that at lower latitudes this family is an important component of the flora, whereas in central Veracruz the family has similar values than the Asteraceae, and at the highest latitude there was a decrease in the value. In the case of the Orchidaceae, our study shows the highest value compared to the other locations, which demonstrates that the forest fragments in central Veracruz harbor a high number of orchids (Castañeda-Zárate *et al.* 2012).

On the other hand, species richness in our study was much lower compared to the numbers presented by Castillo-Campos *et al.* (2007), which is due to the fact that their work was realized in tropical deciduous forest which is recognized as vegetation type with high diversity of herbaceous angiosperms, as well as a more concentrated and exhaustive sampling effort in only one vegetation type. In general, the tropical deciduous forests occur in environments with high light incidence during the dry season (Chiarucci 1994). Besides, the limitations imposed by the bedrock, such as lack of organic matter in the soil, restrict the establishment of other plant groups (e.g., trees). Therefore, the herbaceous layer is facilitated by excluding competitors due to the physiological and functional traits that are characteristic of this plant group (Castillo-Campos *et al.* 2007).

2.5.2 Patterns of richness along the elevational gradient

We found a not very pronounced hump-shaped pattern in the overall species distribution along the elevational gradient (Fig. 2.2), which is a pattern found in different groups of vascular plants along tropical elevational gradients, such as ferns (Salazar *et al.* 2015), terrestrial herbs (Willinghöfer *et al.* 2011) and shrubs (Chawla *et al.* 2008). Rahbek (1995) suggested that the distribution of plants in tropical areas is affected by the high variation of environmental factors that can change substantially in small regions, and this causes differences in the form of distributional patterns. We found that the sea level site was less species-rich compared with the other sites. The following sites (from 650 until 2,100 m) have an intermediate species richness (Fig. 2.2). This is probably due to heterogeneity in their landscape in comparison to other areas of the state, such as the coastal plain, caused by the heterogeneous structure of the physiographic discontinuity generated by the union of two regions: Coastal plain of the Gulf of Mexico and Trans-Mexican Volcanic Belt (Narave-Flores 1985, Torres-Cantú 2013).

The highest species richness was found at 2,500 m, which has been also reported from Ecuador for all endemic vascular plant species, endemic species of Acanthaceae, Asteraceae, Lamiaceae, Piperaceae and Scrophulariaceae (Kessler 2002), and for liverworts in the Northern Andes (Wolf 1993). This pattern is based on a contact of different species assemblages within the transition between two climate zones (Lauer 1973, Wolf 1993) and a high level of humidity due to cloud condensation (Rahbek 1995, Hemp 2005). The richness tends to decrease at higher elevations because productivity and temperature decrease with elevation (Currie *et al.* 2004, Hawkins *et al.* 2007); both factors affect the competition and growth of plants (Vázquez & Givnish 1998). Furthermore, the kind of dominant tree species (*Pinus* spp. and *Abies religiosa*) at the highest sites (3,000 and 3,500 m) has an influence on the herbaceous community because the coniferous litter changes the soil properties (Whittaker 1975, van Wesenbeeck *et al.* 2003).

2.5.3 Forest use intensity effect

The degraded and secondary forests of the 50 m, 650 m, 2,100 m, 3,100 m and 3,500 m sites had higher species richness, compared to the old-growth forests. Furthermore, we found introduced and generalist species most frequently in secondary and degraded forest due to the changes in abiotic factors, such as a drier microclimate, change in soil nutrients and higher light incidence (Köster *et al.* 2009) that allow them to outcompete native species due to specific arrangements of traits (Schultz & Dibble 2012) (Table 2.1, Appendix). Similarly, Firn *et al.* (2011) reported that some herbaceous angiosperms are related to human forest use intensity, which allows the establishment of ruderal species. These species increase the richness in anthropogenically influenced habitats, although native biodiversity is affected negatively by introduced plant species. This indicates that modifications in the structure of the old-growth forest affect the species composition of herbaceous angiosperms because changes in abiotic factors due to forest use intensity may increase the richness, especially of Poaceae and Orchidaceae in degraded habitats, whereas Asteraceae increase in secondary habitats. This is due to the ability of ruderal species to survive or even being favored in drier microclimates (Givnish 1995, Pons & Poorter 2014) with more light in the understory due to the most open canopy of degraded forests (Grime 1977, Lavorel & Grigulis 2011). Consequently, in North American forests, a higher richness of terrestrial herbs was found in the degraded forest with open canopy gaps compared to mature forests with closed canopies (Meekins & McCarthy 2001).

However, the richness of species decreases in the degraded and secondary forests of the 1,600 and 2,500 m sites compared to the old-growth humid montane forest. This similar pattern was found for ferns (Carvajal-Hernández *et al.* 2014, Carvajal-Hernández & Krömer 2015) and in general for vascular epiphytes (Krömer & Gradstein 2003, Köster *et al.* 2009). This loss of species is due to the adaptation of many native species to temperate climate with high humidity (Parry *et al.* 2007). Furthermore, the changes in the structure of soil due to the forest use intensity leads to a loss of microbial organisms that favor the establishment of some species (Camenzind *et al.* 2014). On the other hand, it is widely documented that fragmentation has a negative effect on species richness in lowland forest, especially on understory plants (Magrach *et al.* 2014). For example, in the south of Veracruz, Zambrano *et al.* (2014) found that seeds of understory plants could be affected

by altered microclimatic conditions in the fragmented landscape. These species seem to be adapted to moderate conditions of humidity and temperature which, respectively, decrease and increase with forest use intensity (Dale *et al.* 2001). *Peperomia magnoliifolia* serves as an example in the 650 m site, *Begonia multistaminea* and *P. cobana* in the 1,600 m site, where these are commonly found in habitats of high humidity and shadow (old-growth forest), but probably cannot tolerate high levels of radiation and low humidity and thus are rare in degraded and secondary forests (Ali 2013, Mathieu *et al.* 2015).

It was hypothesized that intermediate forest use intensity leads to higher species richness (Connell 1978, Warren *et al.* 2007) and plant community endemism (Kessler 2001). The mosaic vegetation pattern in our study area is an important shelter for the endemic flora of the region. Since the level of forest use intensity was similar in all sites, the different effects can only be attributed to feedbacks between the specific plant community and the changes in environmental factors, such as microclimate or soil nutrients.

In azonal vegetation (riparian forests), except for the 2,500 m site, the richness was higher than in old-growth forests, which might be due to stable moist environmental conditions and higher soil moisture. In the case of the 650 m site, the species richness recorded in azonal vegetation was almost twice of that observed in the old-growth tropical semi-deciduous forest. This interpretation is consistent with results found by Poulsen and Balslev (1991) in the Amazonian rain forest, who recorded the highest richness of herbs along rivers, which was explained by a mix of species from the border zone to the moist zone next to their study plot and the edaphic and topographic heterogeneity. In the case of terrestrial ferns, Carvajal-Hernández & Krömer (2015) found the same pattern suggesting that fern richness is favored in areas with the influence of water and high humidity. These results confirm the value of the azonal vegetation as reservoirs of biodiversity.

2.5.4 Introduced species

Within the set of introduced species, there is a subgroup known as invasive alien or invasive species, which includes those that survive, are established and reproduce

uncontrollably outside their natural environment, causing serious damage to biodiversity, economy, agriculture and public health (CONABIO 2016). We found several introduced species recognized as invasive, e.g. *Commelina diffusa* is a species that invades cultivated parcels and can endure wastelands inundating, meadows and roadsides areas which are problematical mainly in early yields, but can similarly cause a problem in established yields in Mexico due to its extensive behaviour (Boyette *et al.* 2015). *Oeceoclades maculata* is competing for the same microhabitat and may displace other native terrestrial orchids (Moreno-Molina *et al.* 2014). *Hedychium coronarium* has a negative influence on the recruitment of plants from the plant community, with consequences for the biodiversity of invaded areas (de Castro *et al.* 2016). *Foeniculum vulgare* is particularly aggressive in abandoned agricultural fields and grazed areas (Power *et al.* 2014). *Rumex acetosella* might interfere with secondary succession processes and gap colonization dynamics of native species, and it has the ability to competitively exclude native tussock grasses (Franzese & Ghermandi 2014).

2.5.5 Geographical distribution

In general, the inventoried species show a phytogeographical affinity with southern latitudes, which can be seen by the high number of taxa also occurring in Central and South America. Nevertheless, many endemic taxa of central Mexico have also been encountered. In this context, Rzedowski (2006) suggests that for the flora of *Tierra caliente* (from sea level until ca. 1,400 m) the southern Neotropical affinity dominates over the boreal affinity. In addition, in *Tierra templada*, the most important elements have a southern origin with less boreal elements. In the cooler zones (*Tierra fría* and *Tierra helada*), the most important floristic elements are equally of southern and boreal affinity with some being endemic species from North America, such as *Ageratina pazcuarensis* and *Festuca rosei*, whereas others, such as *Carex melanosperma*, *Corallorhiza maculata*, and *Muhlenbergia macroura* are species endemic to Central America.

Our results show that species richness patterns of herbaceous angiosperms of forest vegetation in central Veracruz are determined by the large environmental gradient of the region. Moreover, degraded and secondary forests exhibit high species richness

depending on the elevational belt, which is probably due to the ability of species in several families that compete better under high light conditions. The high richness and turnover of species, including many endemic elements, highlights the importance of this region for plant conservation; however, this area is also highly threatened by land use changes and shows very high deforestation rates (Ellis & Martínez 2010).

Castillo-Campos *et al.* (2008) proposed to create a system of many protected reserves distributed throughout the state in order to protect this kind of landscape and its flora under the plan of “archipelago reserves” described by Halffter (2005), where all landscape units are connected by small protected areas. In addition, we suggest that an environmental heterogeneity formed by mature, disturbed and secondary forests is acceptable (and unavoidable) and can even increase species richness. This is an opportunity to develop a sustainable management concept to protect and promote species richness and to take into account the need of the local population for forest ecosystem services, such as timber, water, landslide protection, recreation and tourism. This could be an alternative to the current concept of a protected area, such as a national park, that is only focused on protecting alpha diversity without consideration of species turnover rates (Castillo-Campos *et al.* 2008). Thus, it is necessary to create a conservation and management plan for the study area, which requires taking into account more taxonomic groups, the existing proportions of different habitat types, as well as studies on the socio-economic conditions across the elevational gradient.

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2.7 Appendix. Species of herbaceous angiosperms recorded along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico.

Collector: Jorge Gómez Díaz (JGD); Herbaria: MEXU: Instituto de Biología, UNAM; XAL: Instituto de Ecología, A.C., XALU: Facultad de Biología, Universidad Veracruzana, and CIIDIR: Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, IPN. Data are presented for the minimum (min) and maximum (max) observed elevational distribution range, number of plots (N) in which the species was recorded in a total of 135 plots, and conservation/distribution status: T= threatened, P= protected, V= endemic to Veracruz, Mx= endemic to Mexico, Mx1= Megamexico 1, Mx2= Megamexico 2, E=exotic and R= ruderal. Nomenclature follows Tropicos.org (<http://www.tropicos.org>, accessed on 24 Mar 2016).

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
LILIIDAE				
<u>Amaryllidaceae</u>				
<i>Hypoxis</i> sp. 1 (JGD 212, MEXU; XAL)	1,500	1,500	1	
<i>Hypoxis</i> sp. 2 (JGD 260, XALU)	3,100	3,100	2	
<u>Araceae</u>				
<i>Anthurium andicola</i> Liebm. (JGD 329, MEXU)	2,100	2,100	2	Mx2
<i>Anthurium podophyllum</i> (Schltdl. & Cham.) Kunth (JGD 462, MEXU)	50	50	2	T, Mx
<i>Anthurium scandens</i> (Aubl.) Engl. (JGD 175, MEXU)	1,500	1,500	3	
<i>Anthurium schlechtendalii</i> Kunth (JGD 319, XAL)	650	1,000	17	
<i>Anthurium</i> sp. (JGD 369, XALU)	1,000	1,000	1	
<i>Monstera acuminata</i> K. Koch (JGD 444, MEXU)	650	650	3	
<i>Monstera deliciosa</i> Liebm. (JGD 170, MEXU)	1,500	1,500	6	
<i>Philodendron radiatum</i> Schott (JGD 315, MEXU; XAL)	650	650	13	

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Spathiphyllum cochlearispathum</i> (Liebm.) Engl. (JGD 432, MEXU; XAL; XALU)	650	650	2	Mx2
<i>Syngonium macrophyllum</i> Engl. (JGD 321, MEXU)	50	50	1	
<i>Syngonium podophyllum</i> Schott (JGD 312, MEXU)	50	650	16	
<i>Syngonium sagittatum</i> G.S. Bunting (JGD 174, MEXU; XAL)	1,000	1,500	23	Mx
<u>Arecaceae</u>				
<i>Chamaedorea elegans</i> Mart. (JGD 336, XALU)	650	1,000	17	Mx2
<i>Chamaedorea oblongata</i> Mart. (JGD 452, XALU)	650	650	1	
<i>Chamaedorea tepejilote</i> Liebm. (JGD 184, MEXU; XALU)	1,000	2,100	30	
<u>Asparagaceae</u>				
<i>Maianthemum paniculatum</i> (M. Martens & Galeotti) La Frankie (JGD 381, MEXU; XAL; XALU)	2,100	2,100	6	
<i>Maianthemum</i> sp. (JGD 451, XALU)	2,500	2,500	5	
<u>Bromeliaceae</u>				
<i>Aechmea bracteata</i> (Sw.) Griseb. (JGD 316, MEXU; XAL)	650	650	3	
<i>Bromelia</i> cf. <i>pinguin</i> L. (JGD 314, MEXU)	50	50	4	
Cf. <i>Pitcairnia</i> sp. 1 (JGD 268, MEXU)	3,100	3,100	5	
Cf. <i>Pitcairnia</i> sp. 2 (JGD 276, MEXU)	2,100	2,500	5	
Cf. <i>Pitcairnia</i> sp. 3 (JGD 328, MEXU)	650	650	1	
<i>Greigia van-hyningii</i> L.B. Sm. (JGD 330, MEXU)	2,100	3,100	22	Mx
<u>Commelinaceae</u>				
<i>Callisia fragrans</i> (Lindl.) Woodson (JGD 387, XALU)	650	650	3	Mx
<i>Commelina diffusa</i> Burm. f. (JGD 450, XALU)	650	650	1	E, R
<i>Commelina erecta</i> L. (JGD 454, XALU)	650	650	1	R
<i>Gibasis geniculata</i> (Jacq.) Rohweder (JGD 196, MEXU; XAL; XALU)	1,500	1,500	11	
<i>Gibasis linearis</i> (Benth.) Rohweder (JGD 320, XAL)	50	50	1	Mx
<i>Tradescantia zanonii</i> (L.) Sw. (JGD 383, MEXU; XAL)	2,100	2,100	5	
<i>Tripogandra disgrega</i> (Kunth) Woodson (JGD 243, MEXU; XAL)	1,000	2,100	8	Mx2
<i>Tripogandra serrulata</i> (Vahl) Handlos (JGD 302, XAL)	2,100	2,100	12	
<i>Tripogandra</i> sp. (JGD 443, MEXU)	650	650	1	
<u>Cyclanthaceae</u>				
<i>Asplundia</i> sp. (JGD 318, MEXU)	650	650	1	
<u>Cyperaceae</u>				
<i>Carex chordalis</i> Liebm. (JGD 286A, CIIDIR)	2,100	2,500	2	
<i>Carex cortesii</i> Liebm. (JGD 247, XAL; CIIDIR)	1,500	2,500	11	Mx2
<i>Carex melanosperma</i> Liebm. (JGD 162, MEXU; XAL; CIIDIR)	2,500	2,500	3	Mx2
<i>Carex</i> sect. <i>longicaules</i> (JGD 286B, CIIDIR)	2,100	2,100	1	
<i>Carex thurberi</i> Dewey (JGD 323, XAL; CIIDIR)	1,500	1,500	7	
<i>Cyperus articulatus</i> L. (JGD 241, MEXU; XAL; CIIDIR)	50	50	1	R
<i>Cyperus ligularis</i> L. (JGD 286, XAL; CIIDIR)	2,100	3,100	12	
<i>Cyperus manimae</i> Kunth (JGD 185, MEXU)	3,100	3,100	2	R
<i>Cyperus seslerioides</i> Kunth (JGD 155, CIIDIR)	2,500	2,500	1	R
<i>Cyperus surinamensis</i> Rottb. (JGD 201, MEXU; CIIDIR)	1,500	1,500	1	

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Cyperus virens</i> var. <i>minarum</i> (Boeckeler) Denton	1,500	1,500	1	R
<i>Eleocharis geniculata</i> (L.) Roem. & Schult. (JGD 188, MEXU)	650	650	1	E
<i>Eleocharis montana</i> (Kunth) Roem. & Schult. (JGD 322, XAL; CIIDIR)	650	650	1	
<i>Kyllinga pumila</i> Michx. (JGD 166, MEXU; CIIDIR)	1,500	1,500	5	
<i>Rhynchospora radicans</i> (Schltdl. & Cham.) H. Pfeiff. subsp. <i>radicans</i> (JGD 169 & 460, MEXU; XAL; CIIDIR)	1,500	2,100	17	R
<i>Rhynchospora schiedeana</i> Kunth (JGD 303, XAL; CIIDIR)	2,100	2,100	3	
<i>Scleria lithosperma</i> (L.) Sw. (JGD 457, CIIDIR)	650	650	3	
<i>Uncinia hamata</i> (Sw.) Urb. (JGD 458, XAL; CIIDIR)	2,100	2,500	13	
<u>Heliconiaceae</u>				
<i>Heliconia adflexa</i> (Griggs) Standl. (JGD 186, MEXU)	1,500	1,500	1	Mx2
<i>Heliconia schiedeana</i> Klotzsch (JGD 240, XALU)	1,000	1,500	6	Mx2
<u>Iridaceae</u>				
<i>Sisyrinchium scabrum</i> Cham. & Schltdl. (JGD 326, MEXU)	2,500	2,500	1	
<u>Juncaceae</u>				
<i>Luzula</i> sp. (JGD 190, MEXU)	2,500	2,500	4	
<u>Orchidaceae</u>				
<i>Beloglottis mexicana</i> Garay & Hamer (JGD 372, MEXU)	1,000	1,000	1	Mx2
<i>Calanthe calanthoides</i> (A. Rich. & Galeotti) Hamer & Garay (JGD 394, MEXU)	2,500	2,500	7	
<i>Calanthe</i> sp. (JGD 466, MEXU)	2,100	2,100	1	
<i>Corallorhiza maculata</i> (Raf.) Raf. (JGD 295, MEXU)	3,500	3,500	1	
<i>Cyclopogon elatus</i> (Sw.) Schltr. (JGD 406, MEXU)	2,500	2,500	1	
<i>Cyclopogon</i> sp. 1 (JGD 337, MEXU)	650	1,000	5	
<i>Cyclopogon</i> sp. 2 (JGD 373, MEXU)	650	650	1	
<i>Cyrtopodium macrobulbon</i> (La Llave & Lex.) G.A. Romero-Gonzalez & Carnevali (JGD 374, MEXU)	650	650	5	Mx2
<i>Epidendrum radicans</i> Pav. ex Lindl. (JGD 244, MEXU)	1,500	1,500	1	
<i>Goodyera</i> sp. 1 (JGD 391, MEXU)	2,100	2,100	1	
<i>Goodyera</i> sp. 2 (JGD 428, MEXU; XAL)	3,100	3,100	1	
<i>Govenia superba</i> (La Llave & Lex.) Lindl. (JGD 442, MEXU)	2,500	2,500	2	
<i>Govenia</i> sp. 1 (JGD 463, MEXU)	2,100	2,100	1	
<i>Govenia</i> sp. 2 (JGD 282, MEXU)	3,100	3,100	3	
<i>Govenia</i> sp. 3 (JGD 472, MEXU)	650	650	1	
<i>Habenaria floribunda</i> Lindl. (JGD 471, MEXU)	1,500	1,500	2	Mx2
<i>Habenaria novemfida</i> Lindl. (JGD 377, MEXU)	1,500	1,500	1	Mx2
<i>Malaxis excavata</i> (Lindl.) Kuntze (JGD 390, MEXU)	2,100	2,100	1	
<i>Malaxis histionantha</i> (Link, Klotzsch & Otto) Garay & Dunst. (JGD 371, MEXU; XAL)	1,000	1,000	6	
<i>Malaxis soulei</i> L.O. Williams (JGD 427, MEXU)	3,100	3,100	1	
<i>Oeceoclades maculata</i> (Lindl.) Lindl. (JGD 332, MEXU; XAL)	50	1,000	7	E
<i>Pelexia funckiana</i> (A. Rich. & Galeotti) Schltr. (JGD 198, MEXU)	1,500	1,500	10	
<i>Prescottia stachyodes</i> (Sw.) Lindl. (JGD 221, MEXU)	1,500	1,500	5	

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Psilochilus macrophyllus</i> (Lindl.) Ames (JGD 200, MEXU)	1,500	1,500	1	
<i>Schiedeella</i> sp. (JGD 464, MEXU)	2,100	2,100	2	
Spiranthinae (JGD 465, MEXU)	2,100	2,100	2	
<i>Vanilla insignis</i> Ames (JGD 429, MEXU)	650	1,000	2	Mx2
<u>Poaceae</u>				
<i>Aegopogon cenchroides</i> Humb. & Bonpl. ex Willd. (JGD 199, XAL)	1,500	2,500	3	
<i>Agrostis toluensis</i> Kunth (JGD 296, XAL)	3,500	3,500	1	
<i>Andropogon</i> sp. (JGD 310, XAL)	50	50	1	
<i>Aristida</i> sp. (JGD 311, XAL)	50	50	1	
<i>Bouteloua gracilis</i> (Kunth) Lag. ex Griffiths (JGD 301, XAL)	2,100	2,500	6	
<i>Brachypodium mexicanum</i> (Roem. & Schult.) Link (JGD 258, XAL)	3,100	3,100	1	
<i>Brachypodium</i> sp. (JGD 298, XAL)	2,100	2,500	8	
<i>Briza minor</i> L. (JGD 299, XAL)	2,500	2,500	1	E
<i>Bromus exaltatus</i> Bernh. (JGD 300, XAL)	2,500	2,500	3	
<i>Chusquea glauca</i> L.G. Clark (JGD 362, MEXU)	2,100	2,100	6	Mx
<i>Chusquea</i> sp. (JGD 468, MEXU)	2,500	2,500	2	
<i>Dichanthelium dichotomum</i> (L.) Gould (JGD 160, MEXU)	1,500	1,500	14	
<i>Eragrostis</i> sp. (JGD 306, XAL)	1,000	1,000	1	
<i>Festuca amplissima</i> Rupr. (JGD 279, XAL)	3,100	3,100	1	
<i>Festuca rosei</i> Piper (JGD 269, XAL)	3,100	3,100	11	Mx1
<i>Festuca</i> sp. (JGD 305, XAL)	1,000	1,500	3	
<i>Guadua</i> sp. (JGD 307, XAL)	650	650	2	
<i>Hordeum</i> sp. (JGD 234, MEXU; XAL)	1,000	1,500	1	
<i>Lasiacis</i> sp. 1 (JGD 441, XAL)	650	650	1	
<i>Lasiacis</i> sp. 2 (JGD 161, MEXU)	1,500	1,500	6	
<i>Lasiacis</i> sp. 3 (JGD 168, MEXU)	1,500	1,500	2	
<i>Melinis</i> sp. (JGD 308, XAL)	650	650	2	
<i>Muhlenbergia macroura</i> (Kunth) Hitchc. (JGD 297, XAL)	3,500	3,500	10	R, Mx2
<i>Muhlenbergia</i> sp. (JGD 309, XAL)	650	650	2	
<i>Oplismenus</i> sp. (JGD 439, XAL)	650	650	1	
<i>Oryza latifolia</i> Desv. (JGD 440, XAL)	650	650	1	
<i>Otatea acuminata</i> (Munro) C.E. Calderón & Soderstr. (JGD 470, MEXU)	650	650	1	
<i>Panicum</i> sp. (JGD 469, MEXU)	650	650	1	
<i>Paspalum</i> sp. (JGD 362, XALU)	650	650	1	
<i>Pennisetum</i> sp. (JGD 324, XAL)	650	650	1	
<i>Phyllostachys aurea</i> Riviere & C. Riviere. (JGD 214, XAL)	1,500	1,500	2	
<i>Schizachyrium condensatum</i> (Kunth) Nees (JGD 304, XAL)	650	1,000	17	
<i>Stipa ichu</i> (Ruiz & Pav.) Kunth (JGD 467, MEXU)	3,500	3,500	10	R
<i>Trisetum spicatum</i> (L.) K. Richt. (JGD 254, XAL)	3,100	3,100	14	
<i>Zeugites americanus</i> Willd. (JGD 178, MEXU; XAL)	1,500	1,500	2	
Cf. <i>Zeugites</i> sp. (JGD 286C, XAL)	2,100	2,100	1	

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<u>Zingiberaceae</u>				
<i>Hedychium coronarium</i> J. Koenig (JGD 331, XALU)	50	50	2	E, R
Magnoliidae				
<u>Acanthaceae</u>				
<i>Aphelandra scabra</i> (Vahl) Sm. (JGD 449, XALU)	650	650	2	R
<i>Pseuderanthemum alatum</i> (Nees) Radlk. (JGD 453, XALU)	650	650	4	
<i>Ruellia</i> sp. (JGD 368, MEXU; XAL; XALU)	1,000	1,000	5	
Cf. <i>Ruellia</i> sp. (JGD 405, XALU)	650	650	1	
<u>Amaranthaceae</u>				
<i>Iresine diffusa</i> Humb. & Bonpl. ex Willd. (JGD 233, MEXU; XALU)	1,500	1,500	4	R
<i>Iresine</i> sp. (JGD 433, MEXU; XAL)	2,500	3,100	3	
<u>Apiaceae</u>				
<i>Eryngium columnare</i> Hemsl. (JGD 228, XALU)	2,500	2,500	1	Mx
<i>Eryngium proteiflorum</i> F. Delaroche (JGD 267, XALU)	3,100	3,500	5	Mx
<i>Foeniculum vulgare</i> Mill. (JGD 287, MEXU; XALU)	3,100	3,100	2	E, R
<i>Sanicula liberta</i> Cham. & Schltld. (JGD 211, MEXU; XAL; XALU)	1,500	1,500	5	
<u>Araliaceae</u>				
<i>Hydrocotyle mexicana</i> Schltld. & Cham. (JGD 422, XALU)	2,500	2,500	4	
<i>Hydrocotyle umbellata</i> L. (JGD 213, XALU)	1,500	1,500	3	
<u>Asteraceae</u>				
<i>Achillea millefolium</i> L. (JGD 289, XALU)	2,500	3,100	4	E, R
<i>Ageratina chazaroana</i> B.L. Turner (JGD 401, MEXU)	2,500	2,500	2	Mx
<i>Ageratina pazcuarensis</i> (Kunth) R.M. King & H. Rob. (JGD 255, MEXU)	2,500	2,500	1	Mx1
<i>Ageratina pichinchensis</i> (Kunth) R.M. King & H. Rob. (JGD 403, MEXU)	2,500	2,500	2	
<i>Ageratina</i> sp. (JGD 434, XALU)	2,500	2,500	1	
<i>Artemisia ludoviciana</i> Nutt. (JGD 274, XALU)	3,100	3,100	1	R
<i>Bidens</i> sp. (JGD 163, MEXU)	2,500	2,500	1	
<i>Cirsium conspicuum</i> (G. Don) Sch. Bip. (JGD 351, MEXU; XALU)	2,500	2,500	1	Mx
<i>Cirsium ehrenbergii</i> Sch. Bip. (JGD 352, MEXU)	3,100	3,100	11	Mx
<i>Cirsium nivale</i> (Kunth) Sch. Bip. (JGD 253, XALU)	3,500	3,500	3	Mx
<i>Conyza canadensis</i> (L.) Cronquist (JGD 435; XALU)	650	650	5	R
<i>Conyza coronopifolia</i> Kunth (JGD 227, XALU)	1,500	2,500	6	R
<i>Elephantopus mollis</i> Kunth (JGD 205, MEXU; XALU)	1,500	1,500	5	
<i>Hymenoxys integrifolia</i> (Kunth) Bierner (JGD 273, 293 & 361, MEXU; XALU)	2,500	3,500	14	
<i>Laennecia gnaphalioides</i> (Kunth) Cass. (JGD 355, XALU)	2,500	2,500	4	
<i>Pseudognaphalium liebmannii</i> (Sch. Bip. ex Klatt) Anderb. (JGD 270, XALU)	3,100	3,100	8	
<i>Roldana angulifolia</i> (DC.) H. Rob. & Brettell. (JGD 396, XALU)	2,500	2,500	4	Mx
<i>Roldana aschenborniana</i> (S. Schauer) H. Rob. & Brettell (JGD 208, MEXU; XALU)	1,500	1,500	4	
<i>Sabazia humilis</i> (Kunth) Cass. (JGD 395, XALU)	2,500	2,500	4	Mx, R

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Sabazia sarmentosa</i> Less. (JGD 285, XALU)	3,100	3,100	1	
<i>Senecio callosus</i> Sch. Bip. (JGD 283 & 359, MEXU; XAL; XALU)	2,500	3,500	16	
<i>Senecio cinerarioides</i> Kunth (JGD 436, MEXU; XALU)	3,500	3,500	2	Mx
<i>Senecio deppeanus</i> Hemsl. (JGD 206, MEXU; XALU)	1,500	1,500	1	
<i>Senecio roseus</i> Sch. Bip. (JGD 330A, MEXU)	3,500	3,500	1	Mx
<i>Senecio</i> sp. (JGD 411, XALU)	2,500	2,500	1	
<i>Sigesbeckia jorullensis</i> Kunth (JGD 398, XALU)	2,500	3,100	6	R
<i>Trixis inula</i> Crantz (JGD 446, XALU)	650	650	3	
<i>Verbesina robinsonii</i> (Klatt) Fernald ex B.L. Rob. & Greenm. (JGD 445, MEXU; XALU)	3,100	3,100	2	Mx
Cf. <i>Verbesina</i> sp. 1 (JGD 171, MEXU)	1,500	1,500	1	
Cf. <i>Verbesina</i> sp. 2 (JGD 173, MEXU; XALU)	2,100	2,100	1	
<u>Begoniaceae</u>				
<i>Begonia fusca</i> Liebm. (JGD 181, MEXU)	2,100	2,100	1	
<i>Begonia heracleifolia</i> Schltld. & Cham. (JGD 325, MEXU)	650	650	1	
<i>Begonia manicata</i> Brongn. ex F. Cels (JGD 376, XALU)	1,000	1,000	1	
<i>Begonia multistaminea</i> Burt-Utley (JGD 187, MEXU)	1,500	1,500	1	V
<i>Begonia nelumbonifolia</i> Schltld. & Cham. (JGD 386, MEXU; XAL; XALU)	2,100	2,100	2	
<i>Begonia oaxacana</i> A. DC. (JGD 191, MEXU; XALU)	1,500	2,500	6	
<u>Boraginaceae</u>				
<i>Hackelia mexicana</i> (Schltld. & Cham.) I.M. Johnst. (JGD 288 MEXU; XAL; XALU)	3,100	3,100	1	
<i>Macromeria</i> sp. (JGD 400, XALU)	2,500	2,500	2	
<i>Phacelia platycarpa</i> (Cav.) Spreng. (JGD 294, XALU)	3,100	3,100	4	R
Morpho unidentified 1 (JGD 456, MEXU; XAL; XALU)	3,100	3,100	2	
Morpho unidentified 2 (JGD 262, XALU)	2,500	2,500	1	
<u>Brassicaceae</u>				
<i>Pennellia longifolia</i> (Benth.) Rollins (JGD 409, XALU)	2,500	2,500	3	
<u>Campanulaceae</u>				
<i>Centropogon grandidentatus</i> (Schltld.) Zahlbr. (JGD 249, XALU)	2,500	2,500	10	
Morpho unidentified (JGD 278, MEXU)	3,100	3,100	2	
<u>Capparaceae</u>				
Morpho unidentified (JGD 437, MEXU)	3,100	3,100	3	
<u>Caryophyllaceae</u>				
<i>Arenaria lanuginosa</i> (Michx.) Rohrb. (JGD 420, XALU)	1,000	1,000	1	R
<i>Arenaria lycopodioides</i> Willd. ex D.F.K. Schltld. (JGD 257, XALU)	3,100	3,100	8	R
<i>Arenaria oresbia</i> Greenm. (JGD 417, XALU)	2,500	3,100	2	Mx
<i>Arenaria reptans</i> Hemsl. (JGD 423, XALU)	2,500	2,500	14	R
<i>Cerastium arvense</i> L. subsp. <i>molle</i> (Vill.) Arcang. (JGD 265, XALU)	3,100	3,100	1	E, R
<i>Drymaria cordata</i> (L.) Willd. ex Schult. (JGD 384, XAL)	2,100	2,500	3	R
Morpho unidentified (JGD 424, XALU)	3,100	3,100	2	
<u>Crassulaceae</u>				

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Echeveria mucronata</i> Schltld. (JGD 272, XALU)	3,100	3,100	5	Mx
<i>Echeveria rosea</i> Lindl. (JGD 407, XALU)	2,500	2,500	2	Mx
<i>Sedum obcordatum</i> R.T. Clausen (JGD 291, XALU)	3,100	3,100	1	V
<u>Cytinaceae</u>				
<i>Bdallophyton americanum</i> (R. Br.) Eichler ex Solms. (JGD 358, XALU)	50	50	1	
<u>Ericaceae</u>				
<i>Chimaphila umbellata</i> (L.) W.P.C. Barton (JGD 290, MEXU; XAL; XALU)	3,100	3,100	4	
<i>Monotropa hypopitys</i> L. (JGD 410, XALU)	3,500	3,500	1	P
<i>Monotropa uniflora</i> L. (JGD 421, MEXU; XAL, XALU)	2,500	2,500	3	
<i>Pernettya ciliata</i> (Schltld. & Cham.) Small (JGD 431, XALU)	3,500	3,500	2	
<u>Euphorbiaceae</u>				
<i>Acalypha arvensis</i> Poepp. (JGD 366, XALU)	650	650	1	R
<i>Euphorbia cyathophora</i> Murray (JGD 447, XALU)	1,000	1,000	1	R
<i>Euphorbia dentata</i> Michx. (JGD 207, MEXU; XAL; XALU)	1,500	1,500	3	R
<u>Fabaceae</u>				
<i>Lupinus mexicanus</i> Cerv. ex Lag. (JGD 399, XALU)	3,500	3,500	7	Mx
<i>Lupinus montanus</i> Kunth (JGD 354, XALU)	3,500	3,500	1	Mx2
<i>Trifolium repens</i> L. (JGD 292, XALU)	2,500	3,100	17	E, R
<u>Gentianaceae</u>				
<i>Halenia brevicornis</i> (Kunth) G. Don (JGD 402, XALU)	2,500	2,500	2	
<u>Geraniaceae</u>				
<i>Geranium seemannii</i> Peyr. (JGD 263, XALU)	3,100	3,100	2	R
<u>Gesneriaceae</u>				
<i>Achimenes erecta</i> (Lam.) H.P. Fuchs (JGD 339, XALU)	650	650	1	
<u>Gunneraceae</u>				
Morpho unidentified (JGD 397, XALU)	2,500	2,500	2	
<u>Lamiaceae</u>				
<i>Asterohyptis stellulata</i> (Benth.) Epling (JGD 338, XALU)	650	650	1	Mx
<i>Marrubium vulgare</i> L. (JGD 176, MEXU)	2,500	2,500	4	E, R
<i>Prunella vulgaris</i> L. (JGD 426, XALU)	2,500	2,500	1	E, R
<i>Salvia carnea</i> Kunth. (JGD 280, XALU)	3,100	3,100	9	R
<i>Salvia coccinea</i> Buc'hoz ex Etl. (JGD 412, XALU)	2,500	2,500	3	
<i>Salvia hispanica</i> L. (JGD 364, MEXU; XAL; XALU)	1,000	1,000	2	
<i>Salvia iodantha</i> Fernald (JGD 413, XALU)	2,500	2,500	6	Mx
<i>Salvia mexicana</i> L. (JGD 375, XALU)	1,000	1,000	4	Mx, R
<i>Salvia microphylla</i> Kunth (JGD 225, XALU)	1,500	1,500	1	
<i>Salvia polystachia</i> Cav. (JGD 414, XALU)	2,500	2,500	2	
<i>Salvia tiliifolia</i> Vahl (JGD 385, MEXU; XAL; XALU)	2,100	2,100	1	R
<i>Scutellaria racemosa</i> Pers. (JGD 367, XALU)	1,000	1,000	7	
Morpho unidentified (JGD 183, MEXU)	1,500	1,500	1	
<u>Linaceae</u>				

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Linum</i> sp. (JGD 197, MEXU).	1,500	1,500	1	
<u>Lythraceae</u>				
<i>Cuphea aequipetala</i> Cav. (JGD 416, XALU)	2,500	2,500	1	R
<i>Cuphea calaminthifolia</i> Schltld. (JGD 425, MEXU; XAL; XALU)	2,500	2,500	1	Mx
<i>Cuphea salicifolia</i> Schltld. & Cham. (JGD 455, XALU)	650	650	4	Mx
Morpho unidentified (JGD 218, XALU)	1,500	1,500	1	
<u>Malvaceae</u>				
Morpho unidentified (JGD 229, MEXU)	1,500	1,500	1	
<u>Moraceae</u>				
<i>Dorstenia contrajerva</i> L. (JGD 340, XALU)	650	1,000	11	
<u>Orobanchaceae</u>				
<i>Castilleja tenuiflora</i> Benth. (JGD 177, MEXU)	3,100	3,100	1	R
<i>Conopholis alpina</i> Liebm. (JGD 408, XALU)	2,500	2,500	3	
<u>Oxalidaceae</u>				
<i>Biophytum dendroides</i> (Kunth) DC. (JGD 215, XAL)	1,000	1,500	2	
<u>Phytolaccaceae</u>				
<i>Petiveria alliacea</i> L. (JGD 333, MEXU; XAL; XALU)	50	50	1	R
<u>Piperaceae</u>				
<i>Peperomia angustata</i> Kunth. (JGD 392, MEXU)	2,500	2,500	1	
<i>Peperomia arboricola</i> C. DC. (JGD 393, MEXU)	2,100	2,500	4	Mx2
<i>Peperomia cobana</i> C. DC. (JGD 461, MEXU)	1,500	1,500	1	Mx2
<i>Peperomia deppeana</i> Schltld. & Cham. (JGD 231, MEXU)	2,500	2,500	1	
<i>Peperomia donaguiana</i> C. DC. (JGD 189, MEXU; XAL)	1,500	2,500	9	Mx2
<i>Peperomia glabella</i> (Sw.) A. Dietr. (JGD 378, MEXU)	2,100	2,100	7	
<i>Peperomia</i> aff. <i>granulosa</i> (JGD 438, MEXU)	650	650	2	
<i>Peperomia obtusifolia</i> (L.) A. Dietr. (JGD 242 & 473, MEXU; XAL)	650	1,500	13	
<i>Peperomia peltilimba</i> C. DC. (JGD 245, MEXU)	1,500	1,500	1	Mx2
<i>Peperomia subblanda</i> C. DC. (JGD 380, MEXU; XAL)	650	2,100	8	
<u>Plantaginaceae</u>				
<i>Digitalis purpurea</i> L. (JGD 419, XALU)	2,500	2,500	1	E, R
<i>Penstemon gentianoides</i> (Kunth) Poir. (JGD 430, MEXU; XAL; XALU)	3,500	3,500	14	
<u>Polemoniaceae</u>				
Morpho unidentified (JGD 334, XALU)	50	50	1	
<u>Polygalaceae</u>				
Morpho unidentified (JGD 370, XALU)	1,000	1,000	2	
<u>Polygonaceae</u>				
<i>Rumex acetosella</i> L. (JGD 277, XALU)	3,100	3,100	2	E, R
Morpho unidentified (JGD 379, MEXU)	650	650	4	
<u>Portulacaceae</u>				
Morpho unidentified (JGD 335, MEXU)	650	650	3	
<u>Ranunculaceae</u>				

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
<i>Ranunculus multicaulis</i> var. <i>multicaulis</i> T. Duncan (JGD 261, XALU)	3,100	3,100	2	Mx
<u>Rosaceae</u>				
<i>Lachemilla orbiculata</i> (Ruiz & Pav.) Rydb. (JGD 357, XALU)	2,500	2,500	6	
<i>Lachemilla procumbens</i> (Rose) Rydb. (JGD 259, XAL)	3,100	3,100	12	R
<i>Lachemilla vulcanica</i> (Schltdl. & Cham.) Rydb. (JGD 415, MEXU; XAL; XALU)	3,500	3,500	15	
<u>Rubiaceae</u>				
<i>Bouvardia laevis</i> M. Martens & Galeotti (JGD 251, MEXU; XAL; XALU)	2,500	2,500	2	
<i>Coccocypselum hirsutum</i> Bartl. ex DC. (JGD 167, MEXU; XALU)	1,500	1,500	10	
<i>Crusea coccinea</i> DC. (JGD 350, XALU)	2,500	2,500	2	
<i>Deppea grandiflora</i> Schltdl. (JGD 271, XAL)	2,500	3,100	3	
<i>Didymaea alsinoides</i> (Schltdl. & Cham.) Standl. (JGD 388, XALU)	2,100	2,500	4	
<i>Galium aschenbornii</i> S. Schauer (JGD 256, XALU)	2,500	3,100	18	
<i>Hedyotis sharpii</i> (Terrell) G.L. Nesom (JGD 264, XALU)	3,100	3,500	4	Mx
<i>Relbunium hypocarpium</i> (L.) Hemsl. (JGD 474, MEXU)	2,500	2,500	2	
<u>Solanaceae</u>				
<i>Cestrum dumetorum</i> Schltdl. (JGD 448, XALU)	1,000	1,000	1	
<i>Jaltomata procumbens</i> (Cav.) J.L. Gentry (JGD 209, XALU)	1,500	2,500	8	R
<i>Physalis campanula</i> Standl. & Steyerm. (JGD 180, MEXU)	2,100	2,500	3	Mx2
<i>Solanum aligerum</i> Schltdl. (JGD 418, XALU)	2,500	2,500	3	
<i>Solanum demissum</i> Lindl. (JGD 281, XALU)	3,100	3,100	1	
<i>Solanum laxum</i> Spreng. (JGD 404, XALU)	2,500	2,500	2	
<i>Solanum tuberosum</i> L. (JGD 284, XALU)	3,100	3,100	1	E
<u>Valerianaceae</u>				
<i>Valeriana sorbifolia</i> Kunth (JGD 165, MEXU)	2,500	2,500	1	

CHAPTER 3: Diversity and composition of herbaceous angiosperms along gradients of elevation and forest use intensity

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In revision, *Plos One*, submission date September 16th, 2016.



Tropical semi-deciduous azonal forest in *Poza azul*, Palmarejo, Veracruz, Mexico at 500 m.

3 Diversity and Composition of Herbaceous Angiosperms along Gradients of Elevation and Forest Use Intensity

3.1 Abstract

Terrestrial herbs are an important element in tropical forests; however, there is a lack of research on their diversity patterns and how they respond to different forest use intensities. The aim of this study was to analyze the diversity of herbaceous angiosperms along gradients of elevation (50 m to 3500 m) and human forest use intensity on the Eastern slopes of the *Cofre de Perote*, Veracruz, Mexico. We recorded the occurrence of all species of this plant group within 120 plots of 20 m x 20 m. The plots were located in eight study locations separated by ca. 500 m in elevation and within three different habitats: old-growth, degraded, and secondary forest stands ($n = 5$). We analyzed species richness as well as floristic composition in six vegetation belts at different elevations and in different habitats. In total, we recorded 264 plant species, of which 31 are endemic to Mexico. We found some general elevational trends, such as the increase in α -diversity and β_b -diversity and a decline in β_w -diversity. γ -diversity follows a hum-shaped pattern with a peak between 2500 m and 3000 m and a decrease at the extremes. There was no effect of forest use intensity on α -diversity, only β -diversity was different depending on the change of habitat with the highest values when old-growth forest are transformed into secondary forests. Therefore, a loss of a specific forest area is compensated by the occurrence of a similar assemblage at other areas of the same location. The observed high β -diversity, including endemic elements, suggests that a mix of different habitats is needed for reaching high γ -richness of terrestrial herbs.

3.2 Introduction

Our planet is undergoing rapid changes across the majority of biomes, especially in the tropics (Foley *et al.* 2005). Consequently, growing human pressure on ecosystems poses a marked threat to global biodiversity (Godfray *et al.* 2010). Considering current rates of deforestation and forest degradation (Lindenmayer *et al.* 2006), undisturbed forests will

become scarce and increasingly fragmented (Köster *et al.* 2009). Conversion of forest for agriculture as well as non-sustainable agrarian and forestry practices increase the demand for new land, and thus the increase in human population is the main driver threatening primary forests and associated biodiversity (Wright 2005). Whereas the effects of forest conversion on plant diversity are comparatively well known (Gibson *et al.* 2011), there is a lack of knowledge on how anthropogenic forest use intensity affects diversity and composition of plant communities (Flynn *et al.* 2009). Forest degradation may have different effects on biodiversity, depending on the ecosystem, the kind of degradation (temporal and spatial extent, intensity) and the taxa of interest (Gibson *et al.* 2011).

A meta-analysis of global patterns of forest degradation found that there is on average a loss of 22% of terrestrial species richness due to human-mediated forest use (Murphy & Romanuk 2014). According to the analysis, emerging threats for species richness were land-use change and species invasions, followed by temperature increase, habitat loss and nutrient addition (Murphy & Romanuk 2014). Opposed to the global losses, most landscapes, however, experienced a local increase in plant species richness mostly because invasions of exotic species tend to exceed native losses locally (Ellis *et al.* 2012). Therefore, more studies in different ecosystems, e.g. as found along large elevational gradients, are needed to identify the patterns of diversity changes due to forest use intensity (Becker *et al.* 2007).

Little is known about the specific effects of forest use intensity on herbaceous angiosperms despite being an important element of tropical vegetation (Willinghöfer *et al.* 2011). Forest use intensity has been reported to have positive, neutral or negative effects on herb diversity (Mayfield & Daily 2005). Moreover, high numbers of primary forest species and endemic species have been found in naturally regenerating (Barlow & Gardner 2007) and secondary forests, thus, such habitats can provide conservation services (Marin-Spiotta *et al.* 2007). Forest use may also lead to an increase in the number of species due to a suppression of competitive herbs (Buscardo *et al.* 2008). Opposing findings are a consequence of the very different study conditions (biome, ecosystem, taxa of interest), different scales (landscape, plot) and sampling techniques (Naeem *et al.*

2001). Therefore, it is important to carry out more empirical research in order to quantify the effects of forest use intensity on herbs using a robust and replicated study design while accounting for different components of herb diversity (α , β , and γ).

Despite the remaining uncertainties about forest use intensity effects on species richness, changes in species composition have been reported often with the rarest species found mainly in native communities (Cadotte *et al.* 2010). Several studies have shown that with increasing forest use intensity, local (α -diversity) and total (γ -diversity) species richness declined linearly, whereas species turnover within-plots increased. This shows that anthropogenic forest use intensity in the most intensively used plots made the herb layer more sparse and similarly reduced species richness (Decocq *et al.* 2014).

Studies on latitudinal and elevational gradients show that effects of forest use intensity on plant diversity may change depending on the ecosystem or ecozone. Several studies of tropical elevational gradients have shown a peak at mid-elevations in species diversity for various plant groups (McCain & Grytnes 2010). Most works focus on the richest herbaceous families (Krömer *et al.* 2013) and were conducted in near-natural ecosystems. Considering the ongoing conversion of primary into degraded and secondary vegetation types (Gibson *et al.* 2011), studies on elevational gradients have to be advanced by focusing on habitats with different anthropogenic influence.

The objective of this study was to investigate the patterns of diversity (α , β , and γ) of herbaceous angiosperms along a combined gradient of elevation and forest use intensity in order to fill the gap on basic information about herbaceous angiosperms along elevational gradients in the tropics and to identify the factors determining its current composition. The study was implemented at the Eastern slopes of the volcano *Cofre de Perote* in central Veracruz, Mexico. The elevational gradient stretches from sea level up to 3500 m above sea level and exhibits a large range of environmental conditions on c. 80 km horizontal distance. We established plots at eight different locations (separated by c. 500 m in elevation) and in three different forest use intensity types (old-growth, degraded, and secondary forest). We hypothesized that (1) forest use intensity affects herb species richness, (2) there is a continuous turnover in species composition from old-

growth over degraded to secondary forest, and (3) β -diversity within habitats is lower than β -diversity between habitats due to the forest heterogeneity.

3.3 Methods

3.3.1 Study area

The study was conducted at eight sites along an elevational gradient between 30 and 3540 m on the Eastern slopes of the *Cofre de Perote*, an extinct volcano of 4282 m elevation in the central part of the state of Veracruz, Mexico (Fig. 3.1). This region is located at the junction of the Trans-Mexican volcanic belt and the *Sierra Madre Oriental*, a mountainous area between 19° 25' 5.7" and 19° 36' 54" N and 94° 44' 43.5" and 97° 9' 36.9" W. The state of Veracruz covers 72420 km² and hosts a large number of angiosperms (6876 species) representing about 31% of the Mexican flora (Luna-Vega & Espinosa 2013). More than 80% of Veracruz' primary vegetation has been converted and the remaining parts are highly fragmented (Muñoz-Villers & López-Blanco 2008). Veracruz is therefore recognized as a priority region for conservation within Mexico (Williams-Linera 2002).

The study locations were selected at the following elevations above sea level: 30-50 m, 610-670 m, 900-1010 m, 1470-1650 m, 2020-2230 m, 2470-2600 m, 3070-3160 m and 3480-3540 m (Table 3.1, Fig. 3.1). To simplify, from now on we will refer to every site as a categorical unit (50, 650, 1000, 1500, 2100, 2500, 3100, 3500 m). Information about geographical reference and elevation were recorded using a Garmin® GPSMAP 60Cx device.

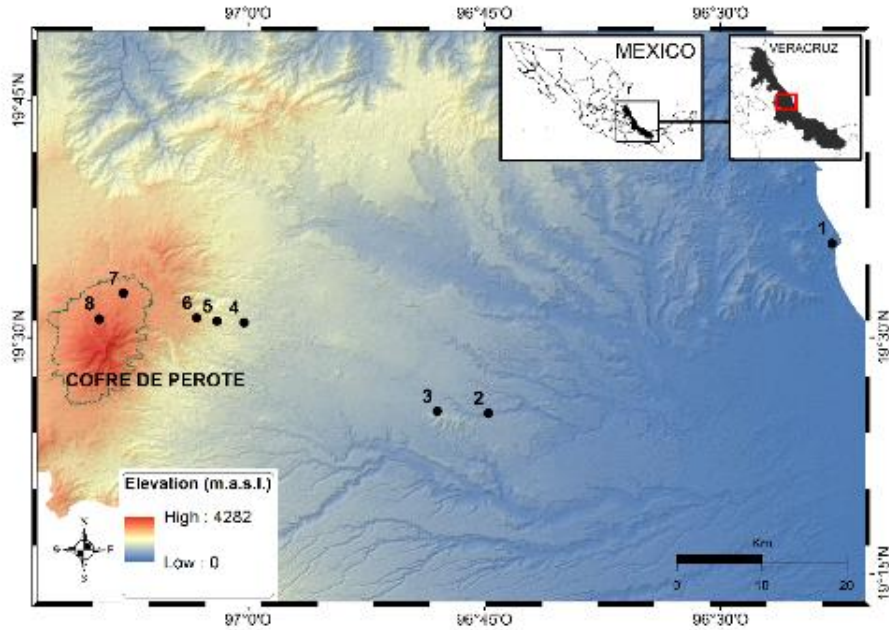


Figure 3.1 Map of the Eastern slopes of the *Cofre de Perote* in Veracruz State, Mexico. Study locations are shown by black dots. 1 = *La Mancha*, 2 = *Palmarejo*, 3 = *Chavarrillo*, 4 = *Los Capulines*, 5 = *El Zapotal*, 6 = *El Encinal*, 7 = *Los Pescados*, and 8 = *El Conejo*.

Table 3.1 List of the study locations along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico. Information is given on elevational range, vegetation type according to Leopold (Leopold 1950), mean annual temperature (MAT), mean annual precipitation (MAP), days of rain (DR), and days below 0°C according to National Meteorological Service of Mexico (data from 1951-2010) (SMN 2016).

Location	Elevation (m)	Vegetation type	MAT (°C)	MAP (mm)	DR	DB
<i>La Mancha</i>	30-50	Tropical semi-humid deciduous forest	26	1221	81	0
<i>Palmarejo</i>	610-670	Tropical semi-humid deciduous forest	23	938	86	0
<i>Chavarrillo</i>	900-1010	Tropical oak forest	21	1552	123	0
<i>Los Capulines</i>	1470-1650	Humid montane forest	18	1598	145	0
<i>El Zapotal</i>	2020-2230	Humid montane forest	14	3004	199	3
<i>El Encinal</i>	2470-2600	Pine-oak forest	12	1142	100	12
<i>Los Pescados</i>	3070-3160	Pine forest	10	821	113	14
<i>El Conejo</i>	3480-3540	Fir forest	8	829	112	16

3.3.2 Field sampling

Fieldwork was conducted between February 2012 and January 2014. We sampled the presence/absence of terrestrial herbaceous angiosperms, which were defined as plants that have no persistent woody stem above ground or plants that are only slightly woody, rooted on the forest floor and have a short height (generally < 1 m); vines were excluded (Poulsen 1996). We recorded all species in 20 m × 20 m plots, without considering seedlings (Carvajal-Hernández & Krömer 2015). A plot size of 400 m² was selected because the area is representative for the flora of the herb families in humid tropical forests but small enough to minimize the variation of abiotic factors (Kessler & Bach 1999). Additionally, this plot size has been used for several comparative studies in the tropics (Cicuzza *et al.* 2013). Plots were located in the three different habitats subjected to different degrees of forest use intensity: old-growth (OG), degraded (DE), and secondary forest (SE) stands (n = 5 plots for each habitat). These categories follow Newbold *et al.* (2015) and are defined in Table 3.2. Each habitat was present at each of the eight locations resulting in a total number of 120 plots and a sampled area of 48000 m². A plant collection permit that covered the whole study area and even allowed us the collection of protected species mentioned in the Mexican legislation (NOM-059-SEMARNAT-2010) was issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT SGPA/DGVS/2405/14), which is the government agency responsible for regulating matters related to nature.

Table 3.2 Classification of habitats with different forest use intensities according to the main physiognomic characteristic, the gap fraction in the canopy, dominance of canopy trees, the percentage of shrubs, and the presence of lianas (Newbold *et al.* 2015).

Habitat	Characteristic	Gaps (%)	Forest use intensity	Canopy trees	Shrub (%)	Lianas
Old-growth	No obvious forest use, dominance of mature trees	<10	Low	High	<30	No
Degraded	Selective logging, grazing and understory removal	11-25	Medium	Low	30-50	Low
Secondary	Regrown after clear-cut	>25	High	very low	>50	High

Throughout the manuscript, we use specific terms regarding the sampling design, which are defined in figure 3.2.

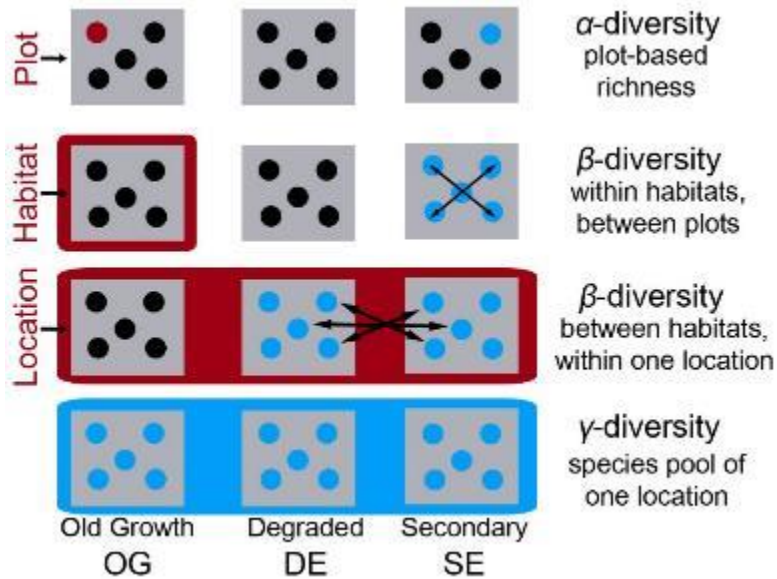


Figure 3.2 Schematic representation of the sampling design. α -diversity is measured in plots of 20 m x 20 m and is given as a mean of five plots. Five plots represent one habitat. Habitat is defined here as a homogenous type of forest use intensity within one location. A location is representative of an elevational belt and harbors three different habitats (OG, DE, and SE). β -diversity was measured in two ways based on pairs of plots. Within-habitat β -diversity represents the compositional heterogeneity of a habitat. It is measured as the 1-Sørensen index based on multiple pairwise comparisons of the five plots within each habitat of a specific location. Between-habitat β -diversity represents the compositional heterogeneity between different forest use intensity. Measurement is similar to within-habitat β -diversity, but multiple pairwise comparisons based on the plots between habitats of a specific location. γ -diversity is defined as the total number of the local species pool across all 15 plots within a location, i.e. three habitats with five plots each.

3.3.3 Species identification

At each location, but not in every plot, specimens of all species were collected and prepared if possible in triplicate and deposited at the Mexican herbaria CIIDIR, MEXU, XAL, and XALU. Details about species identifications, geographical distribution, and classification can be found in Gómez-Díaz *et al.* (accepted).

3.3.4 Data analyses

3.3.4.1 Alpha diversity

Generalized Linear Models (GLMs) were used to assess the effect of the explanatory variables to α -diversity. Plot-based species richness (α -diversity) between locations and habitats was used as the response variable. “Elevation” (continuous) and “habitat” (a factor with three levels “OG”, “DE”, and “SE”), as well as their interaction, were used as explanatory variables in regression models.

α -diversity was modeled as count data using a Poisson error family according to the Shapiro-Wilk normality test ($W = 0.958$, $p = 0.001$) and the “descdist” function of the R package “fitdistrplus” version 1.0-7. α -diversity presented overdispersion ($z = 2$, $p = 0.023$, $\alpha = 0.341$) according to the Test for Overdispersion in the Poisson model (Cameron & Trivedi 1990) tested with the function “dispersiontest” of the R package “AER” version 1.2-4. Therefore, we used the negative binomial GLM family error with a log-link function, which is a model used for continuous variables, usually with over-dispersion using the R package “MASS” version 7.3-45 (Venables & Ripley 2002). All analyses were performed in R 3.2.1 (R Core Team 2014).

We fitted several GLMs using the first to fourth order polynomials of the variable “elevation” and used the Akaike Information Criterion (AIC) (Borcard *et al.* 2011) as the measure of model support, where smaller values indicate a stronger support. We selected the GLM with the fourth order polynomial of “elevation” (AIC = 598.954) for additional analyses because it received the strongest support as an explanatory variable for α -diversity, whereas all other combinations had a higher AIC or failed in some combination.

3.3.4.2 Beta diversity

In order to have a more intuitive β -diversity, we used the dissimilarity (1-S) variant of the Sørensen index (Dice 1945):

$$\beta\text{-diversity} = 1-S \quad \text{Equation 1}$$

where S is the Sørensen index:

$$S = 2C/A+B \quad \text{Equation 2}$$

which is a coefficient of association, where a value of 1 shows that a pair of plots under consideration has exactly the same species. The Sørensen index can be adjusted to measure species turnover (effective or real) (Tuomisto 2010). The index $1-S$ is also a measure of β -diversity because if a coefficient is near to 1, it shows that the units do not share species, and, therefore, they have high β -diversity (Anderson *et al.* 2006).

As a measure for landscape-scale β -diversity, we compared the effect of habitats on floristic composition between OG and DE, OG and SE as well as DE and SE at each site (Chao *et al.* 2005). The calculation was done plot-by-plot, i.e. each plot of habitat A was compared to five or four (in the case of within β -diversity) other plots of habitat B. Additionally, we calculated the standard errors for the β -diversity estimator, letting statistically rigorous contrast of two or other similarity index values. Standard errors were calculated by a bootstrap process, which needs resampling the observed data for pairs of samples and recomputing the estimators N times (Chao *et al.* 2005). All analyses of β -diversity were performed in EstimateS 9.1.0 (Colwell 2013).

We also computed multiple GLMs to explore explanations for elevational patterns of β -diversity. The quasi-binomial error family was used for the models which is appropriated for continuous variables that range from 0 to 1. Therefore, all models were compared by means of an ANOVA test due to the lack of AIC value and log-likelihood in the quasi-binomial family error. The AIC is not displayed for quasi-binomial models because there is not explicit log-likelihood to be maximized as in the case of other error families (Rao & Rao 2014). Also, test statistics from such models should be constructed on F-tests rather than chi-squared tests (Logan 2010). The model with least residual differences and deviation was the quadratic model.

β -diversity indices were compared with a GLM with a quasi-binomial family error. The independent variables were “location” with seven levels (the 50 m location was not analyzed due to the lack of species in six plots) and “habitat transition” with six levels (“OG to OG”, “OG to DE”, “OG to SE”, “DE to DE”, “DE to SE”, and “SE to SE”) and the interaction of both variables. Data was checked for normality using the Shapiro-Wilk normality test. Homogeneity of variance was checked using the Bartlett test. All analyses were performed in R 3.2.1 (R Core Team 2014).

3.3.4.3 Additive gamma partitioning

We used additive partitioning of gamma into alpha and beta components because it has been established as a useful measure to quantify different aspects of communities (Chao *et al.* 2012), is an intuitive measure of diversity that reflects the species turnover, and represents the specifically species diversity similar as does real gamma diversity (Tuomisto 2011). The total observed diversity γ_{obs} , for each habitat type and location, was partitioned as:

$$\gamma = \alpha_1 + \beta_b + \beta_w \quad \text{Equation 3}$$

where α is the mean α -diversity per location, β_b is the between-habitat β -diversity, β_w the mean within-habitat β -diversity. These values can be obtained as follows:

$$\alpha_i = \sum_{j=1}^{n_i} D_{ij} \quad \text{Equation 4}$$

where D_{ij} are the diversity metrics recorded in each sample $j = 1, 2, 3 \dots n_i$ is the number of samples taken at level i of the hierarchical sampling design.

$$\beta_b = \alpha_{i+1} - \alpha_i \quad \text{Equation 5}$$

$$\beta_w = \gamma - \alpha_m \quad \text{Equation 6}$$

to extend across multiple scales, we have a hierarchical design with $i = 1, 2 \dots m$ levels of sampling. Samples in the lowest hierarchical level $i = 1$ represents the smallest sampling unit nested within samples at $i = 2$, and samples at $i = 2 \dots m$ are formed by pooling together the appropriate groups of nested samples from each level $i - 1$ (Crist *et al.* 2003). Analysis of additive diversity partitioning was done using the “hierDiversity” package (Marion *et al.* 2015).

3.4 Results and Discussion

3.4.1 Alpha diversity

Elevation was the only significant predictor of α -diversity of herbaceous angiosperms and explained almost two third of the variance (GLM, $R^2 = 0.59$, $p = 0.003$). α -diversity followed

a bimodal pattern, showing a first peak at 650 m and another at 2500-3100 m, followed by a decline towards the extremes of the gradient (Fig. 3.3).

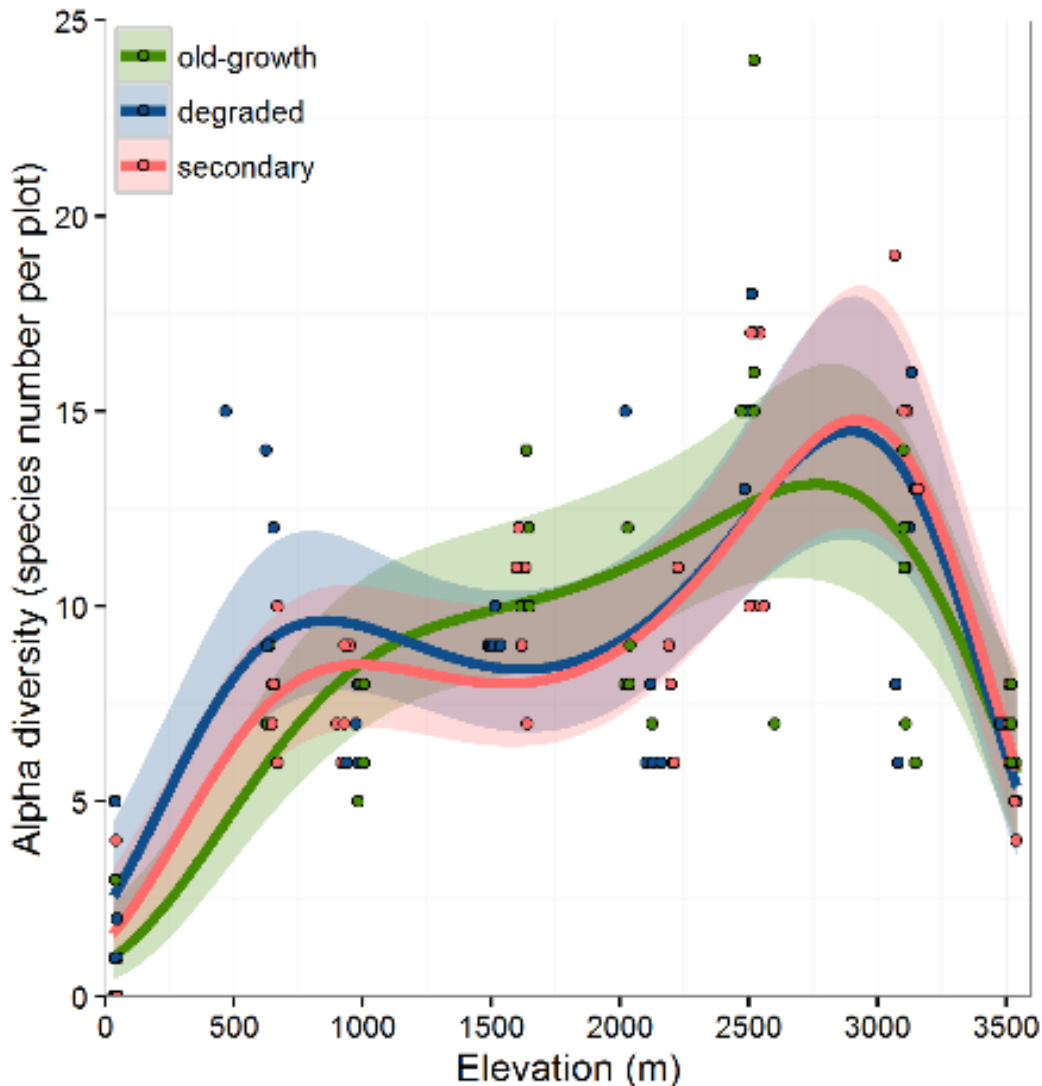


Figure 3.3 α -diversity of herbaceous angiosperms along gradients of elevation and forest use intensity at the *Cofre de Perote*, central Veracruz, Mexico. The lines were fit from a negative generalized linear model (GLM), the shaded area marks confidence intervals (CI = 1.96 times standard error). Difference to zero is not significant for the intercept (xy, OG at 50 m, $p = 0.766$) neither for the effect of habitat (DE: $p = 0.081$, SE: $p = 0.422$). All the effects are estimated in relation to OG. Elevation significantly ($R^2 = 0.59$, $p = 0.003$) affected α -diversity. Observed species richness on 20 m \times 20 m plots along the elevational gradient for OG (green), DE (blue), and SE (red).

Bimodal diversity patterns have been reported for different groups of vascular plants (McCain & Grytnes 2010), such as palms, Acanthaceae, Bromeliaceae and woody plants along tropical mountains (Lovett *et al.* 2006, Eiserhardt *et al.* 2011, Salas-Morales & Meave 2012). However, our results show differences in previous findings as the peak in species richness shifted towards higher, instead of mid-elevations (Kluge & Kessler 2006). Our transect is located near the border of the tropics, whereas most other studies were located within the moist inner tropics.

Lower elevations in Veracruz are subject to prolonged dry seasons (Table 3.2). With increasing elevation, precipitation increases while potential evapotranspiration decreases with lower temperatures. Species richness of ferns has been reported to be positively related to humidity (Salazar *et al.* 2015). In our study, angiosperm richness peaked between 2500 m and 3100 m, where precipitation and number of rainy days already decrease. However, the pine-oak forests at 2500 m are often subject to fog, whereas in pine forests (3100 m) light transmission to the forest floor is high (Holeksa *et al.* 2007), which likely increases the ground cover of angiosperms and thus also their diversity.

Surprisingly, forest use intensity had no significant effect on α -diversity (Fig. 3.3). The lack of a detectable net-change in α -diversity might indicate that the level of forest use intensity is still relatively moderate; however, other life forms (e.g. trees, epiphytes, and ferns) might show contrasting patterns. It is quite well documented that forest herbs profit from better light conditions in DE or SE. Newbold *et al.* (2015) found that the richness of vascular plant species can increase by 40% due to the conversion of old-growth forests to secondary vegetation, but more severe habitat conversion, e.g. from forest to intensive cropland, decreases species richness.

3.4.2 Beta and gamma diversity

Instead of richness, forest use intensity affected the floristic composition. Community composition was markedly affected by habitat transitions (Table 3.3). Within-habitat β -diversity was generally lower (0.42-0.52) than between-habitat β -diversity (0.58-0.66). Not surprisingly, the highest dissimilarity was found in the transition from OG to SE, whereas the most homogenous species pool was within OG. Wider environmental differences are

indicated by the high β -diversity between habitats (Wang *et al.* 2003), than the heterogeneity of plots within the same habitat type.

Table 3.3 Average effects of the habitat change. Mean β -diversity at every habitat transition, letters in superscript differences in groups after Tukey posthoc test (HSD = 0.138).

Habitat transition	β -diversity (1-S)
Old-growth to secondary	0.66 ^a
Degraded to secondary	0.61 ^{ab}
Old-growth to degraded	0.58 ^{ab}
Degraded to degraded	0.52 ^{bc}
Secondary to secondary	0.48 ^{bc}
Old-growth to old-growth	0.42 ^c

There was a marked effect of elevation on β -diversity (Fig. 3.4). Within-habitat β -diversity showed a clear humped-shaped pattern for OG and SE with peaks between 1500 m and 2500 m. DE, however, had their highest β -diversity at 650 m with a subsequent decline. Obviously, DE at lower elevations exhibits a different response to environmental conditions compared to OG and SE. Maybe degradation leads to a higher heterogeneity of environmental conditions and, consequently, offers diverse niches triggering differences in community assemblage (Warren *et al.* 2007). β -diversity between-habitat was generally high but varied with the type of habitat transition. During the transition from OG to SE ca. 50% of species were exchanged at both extremes of the elevational gradient. Between 1500 m and 2500 m, however, even 75% of the species were different after conversion from OG to SE. Habitat transitions related to degradation (OG-DE, DE-SE) showed highest β -diversity between 650 m and 1500 m and declined afterward. Especially at 3100 m and 3500 m, the change in species composition with the transition from OG to DE is relatively low. This indicates that present environmental conditions favor a spectrum of adapted species (Sánchez-González & López-Mata 2003), which thrive regardless of the habitat type. Above 3100 m there are fewer species, which are adapted

to extreme climate events, such as days below 0°C, lower temperature, and precipitation (Table 3.1).

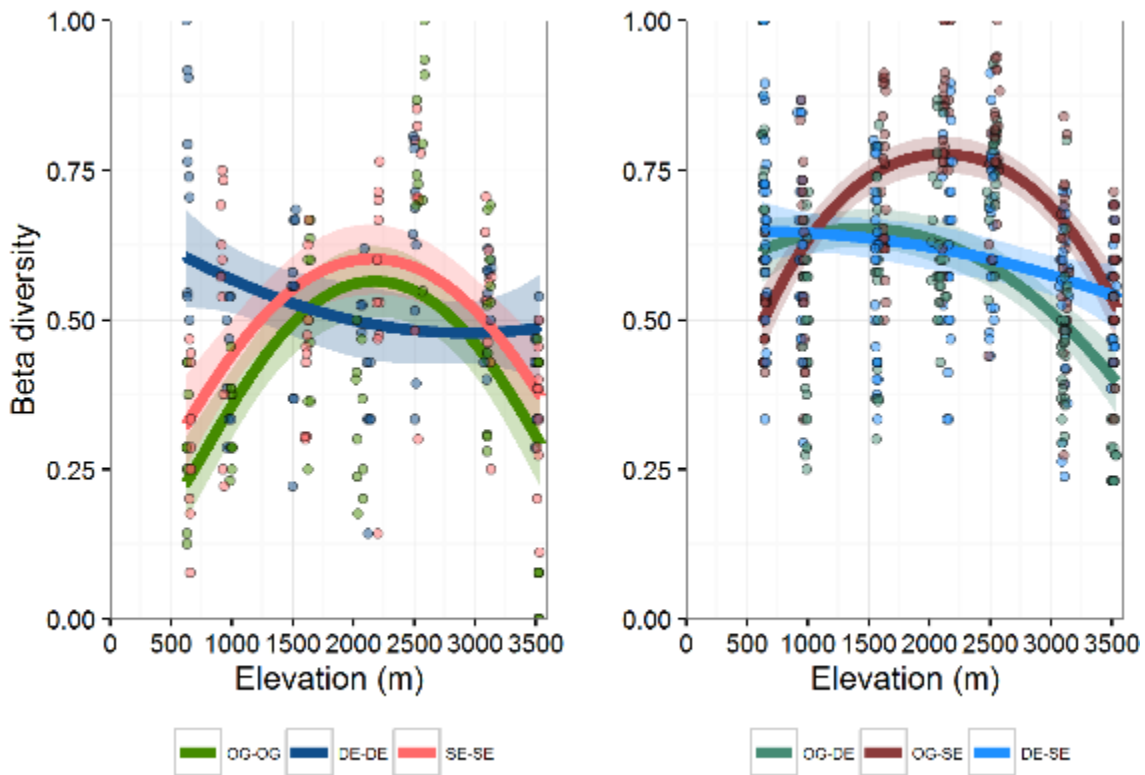


Figure 3.4 Compositional heterogeneity (as a measure for β -diversity) between different changes in forest habitats along the elevational gradient at the *Cofre de Perote*, central Veracruz, Mexico. Values are 1-Sørensen values as means across all plots. Error bars are standard errors computed by a GLM with quasibinomial error family.

The relative contribution of α , within-habitat β , and between habitats β -diversity to γ was revealed by using the additive partitioning approach (Fig. 3.5). The contribution of α -diversity was only between 12% and 32% (Fig. 3.5). The majority of entire species richness was accounted for β -diversity. In general, the values of β -diversity are higher between-habitat (β_b) than within-habitat (β_w). At the landscape scale, plant species diversity is typically accumulated (equal to the location-scale in the current study), this outcome verifies similar preceding results (Chandy *et al.* 2006, Clough *et al.* 2007, Wang *et al.* 2014). Diverse forest habitats support high species diversity and lead to high β -

diversity between-habitat (β_b) confirming the importance of these habitats. There are some general elevational trends, such as the increase in α -diversity and β_b -diversity as well as a decline in β_w -diversity. The increase of α -diversity with elevation could be due to the adaptation of some herbs to cold climates (Hawkins *et al.* 2011), which is similar to the pattern found by Cicuzza *et al.* (2013). A similar pattern of increasing β -diversity was found by Yang *et al.* (2016), which is due to changes in climatic variables since elevation-related vegetation zones reflect climatic zones. This can be also observed in our pattern since the most remarkable changes in values of β_b -diversity are located between different climatic zones (Fig. 3.5), which according to with Yang *et al.* (2016) “shows the effects of an elevation-related climate gradient on β_b -diversity patterns”. The decline in β_w -diversity is consistent with the pattern found by Akhtar & Bergmeier (2015), which is explained by the increasingly controlling effect of climate over other environmental factors (e.g. soil factors) and the decrease of forest heterogeneity at higher elevations.

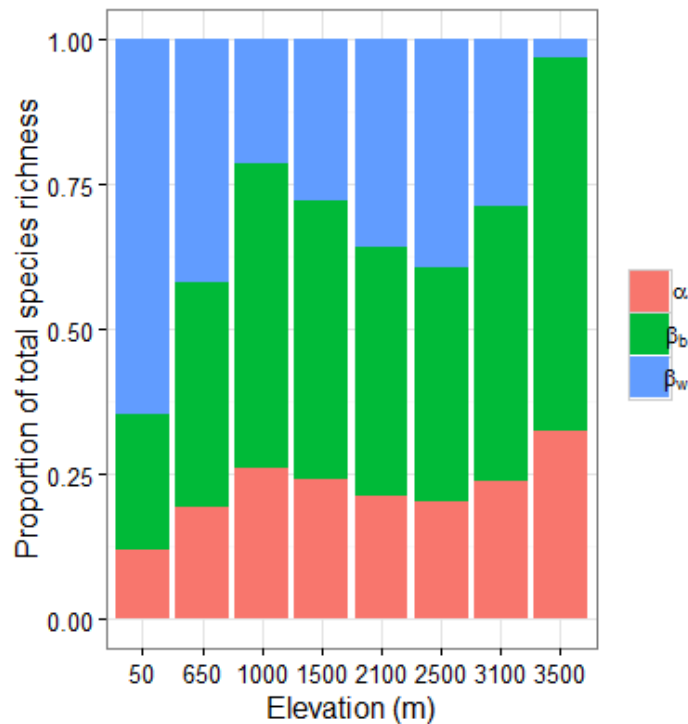


Figure 3.5 Additive gamma partitioning. The total observed diversity partitioned at each habitat type and location (α = α -diversity, β_b = β -diversity between habitats, and β_w = β -diversity within habitats).

The most remarkable effect of forest use intensity was on β -diversity and it was highest between 2100 m and 2500 m (Fig. 3.4). It has been reported that forest use intensity decreases β -diversity due to the propagation of exotic and opportunist species that can lead to a 'biotic homogenization' (Vellend *et al.* 2007). β -diversity is, on average, in our sample of landscapes, lower within habitats than between habitats (Table 3.3 and Fig. 3.4 and 3.5). Also, the α -diversity in our study did not change, but the dissimilarity between habitats was high (0.594 to 0.665) (Table 3.3).

Here, we argue that man-made habitats markedly contribute to the herbaceous angiosperm richness in our study region. It is, of course, important to note that our study does not include spatially weighted information about the abundance of different forest habitats. Pressure on the primary or OG forest is often higher than their ability to regenerate. Therefore, there is the risk that OG or even DE will be converted into SE (Brown & Lugo 1990). Although different successional stages of SE may also harbor high species richness (Valencia *et al.* 2016), our results indicate that OG species are particularly threatened by habitat conversion. A homogenization of habitats will consequently lead to species homogenization by decreasing β -diversity.

The most vulnerable location is the pine-oak forest at 2500 m because high β_b -diversity implies that there is a loss of many OG species during forest degradation. This means that conversion of a certain area increases the chance that a unique flora is changed in composition and invasive species appear. In addition, this elevation contains the largest number of endemic species compared to the rest of locations (Gómez-Díaz *et al.* accepted), leading to increased vulnerability. Therefore, the pine-oak forest at 2500 m should be considered as a priority for conservation, especially because according to Mittermeier *et al.* (Mittermeier *et al.* 2005) this vegetation type in Mexico has the lowest levels of protection (Gómez-Mendoza & Arriaga 2007). For the herbaceous angiosperm group, however, it seems that a well-designed management plan instead of pure conservation would be beneficial because high habitat heterogeneity is required to achieve high species richness.

3.5 Conclusions

Understanding how forest use intensity and elevation affect the species diversity and community composition of herbs is a complex question and needs a frame that allows understanding the different patterns at the landscape level. Therefore, we focused on the three components of diversity (α , β , and γ). We did not find significant differences in α -diversity among the three forest systems, a finding that is not in accordance with previous studies. However, forest use intensity affected the floristic composition, which varied markedly between habitats. The most important component driving γ -diversity was the β -diversity between habitats. Thus, different forest use intensities, which coexist, increased the species richness in the landscape.

Some elevations, and especially the location at 2500 m, were shown to be vulnerable, whereas species richness still depends on a certain degree of forest use intensity. Our findings clearly showed that OG at mid-elevations contributed more to regional diversity than DE. At least for the group of herbaceous angiosperms, sustainable forest management, such as forest certification instead of strict protection may be a good way to conserve herbaceous forest plants in the region. The important influence of β -diversity to regional species richness should be considered in forest protection systems rather than put emphasis completely on the protection at local scale (α) diversity.

3.6 Acknowledgements

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CHAPTER 4: Long-term changes in the forest cover in central Veracruz, Mexico since the 1990s

Jorge Antonio Gómez-Díaz, Kristina Brast, Jan Degener, Thorsten Krömer, Gerhard Gerold and Felix Heitkamp.



Habenaria floribunda Lindl. in humid montane secondary forest in Los Capulines, Tlaxiahuayocan, Veracruz, Mexico.

4 Long-term changes in the forest cover in central Veracruz, Mexico since the 1990s

4.1 Summary

Forest fragmentation and deforestation are important threats for the conservation of species that have severe consequences for ecosystem functions. The focus of this study is to empirically elucidate forest land cover transformations by determining deforestation rates between 1993 and 2014 and recognizing forest types that have the main conversion rates. Our study area is located between 96°-97° W and 19°-20° N in “La Antigua” and “Actopan” drainage basins, which is in the state of Veracruz, Mexico. Historical land cover information for the years 1993, 2000 and 2014 were obtained from image data of Landsat. We applied a supervised classification using maximum likelihood estimation and quantified both the net change in forest area and the loss of original forest area. Landscape metrics were established to measure the spatial shape of the forest fragments. Our results show that the area covered by original forests decreased during the period studied by approximately 57%. The annual net forest change rate for the first period (1993-2000) was -0.44%; and increased significantly to 0.11% for the second period (2000-2014). The old-growth forests of Central Veracruz have suffered high land use change rates throughout the last twenty years with a reduction of this process during the last decade. We found that fragmentation patterns varied considerably between different time periods. In the first period, forest patches increased in irregularity, isolation, and amount, with a reduction in the dimension of patches reflecting the continuing fragmentation of forest habitats. The second period (2000-2014) experienced a slightly recovering of forest cover (+0.11%). Our paper provides a thorough analysis of the forest transformations in Central Veracruz that will increase the consciousness of stakeholders for proper planning and management to maintain biological integrity of the area.

4.2 Introduction

Two critical components of global change are forest fragmentation and deforestation (Tapia-Armijos *et al.* 2015). Thus, together with the degradation of tropical forests, those are the major threats for the conservation of species and have severe consequences for ecosystem functioning (Malhi *et al.* 2008). Some of the consequences of deforestation are changes in habitat quality and structure of ecosystems (Collinge 1996), an increase of greenhouse emissions (Crutzen 2006), degradation of ecosystem services (Chazdon 2008) and species extinctions (Whitmore & Sayer 1992). Forest landscape structure is affected by deforestation due to the decrease of forest area (Foley *et al.* 2005). Most of the forest patches are reduced in size and connectivity due to fragmentation (Andr n 1994). Fleshing out the dynamics of forest transformations within the tropics and sub-tropics will make aware stakeholders on improving carbon storage in existing forest estates.

Half of Mexico's natural forest cover has been lost unevenly in the previous 50 years (Barsimantov & Kendall 2012). However, during the last 20 years, Mexico has decreased deforestation rates (yearly rates of 0.56% for the 1990–2000 period and 0.21% for the 2001–2010 period) (FAO 2014a, Skutsch *et al.* 2014). As in other tropical countries, the main drivers of continuing land cover changes are agricultural expansion, pasture expansion, growing economic inequality and population numbers, timber production, the absence of well-defined property rights, maize cultivation, cattle grazing, highway building and the harvesting of timber (Cortina-Villar *et al.* 2012, Bonilla-Moheno *et al.* 2013). Recently, the Mexican deforestation rates have been reduced due to protection efforts in communal forests (*ejidos*) (Bonilla-Moheno *et al.* 2013) and improving in protection initiatives (Pfaff *et al.* 2014). However, there still some inconsistencies in the available literature for example there some authors that show that the decrease in Mexico's deforestation rates is just a result of methodology inconsistencies (Skutsch *et al.* 2014).

In Mexico, tropical forests and pine-oak forests (mainly found in mountainous regions) have the highest deforestation rates stated to date (Barsimantov & Kendall 2012). Central Mexico is assumed to play a leading role in deforestation in the country (L pez-Barrera *et al.* 2014). However, with the exception of the studies of L pez-Barrera *et al.* (2014) and

Galicia et al. (2013) data on deforestation rates in this area are scarce. Though, the aforementioned studies were only focused on one vegetation type. Furthermore, this area is of specific value and attention for biodiversity preservation (Sarukhan et al. 2014).

The biodiversity of Veracruz has a high degree of endemism and poses a very specific flora, which varies evidently from the rest of the country (Sosa et al. 1998). Unfortunately, deforestation and poaching had extirpated some species from Veracruz such the harpy eagle (*Harpia harpyja*) (Vargas G et al. 2006) and the thick-billed parrot (*Rhynchopsitta pachyrhyncha*) (Sánchez Mateo 2007). The mountainous region of Central Veracruz hosts very important ecosystems, such as humid montane and pine-oak forests, which are very rich in biodiversity and offer a variety of ecological services (Williams-Linera et al. 2007). This region has an outstanding high regional plant diversity resulting from a characteristic high beta diversity or species turnover (Williams-Linera et al. 2007). Also, this region has been proposed to be protected as a natural reserve, an archipelago reserve, which should promote the conservation and restoration of biological landscape corridors connecting forest fragments through riparian forests, and biodiversity-friendly agricultural land, such as shade coffee plantations (Williams-Linera et al. 2007).

High rates of deforestation have been reported by current studies on small zones in this area (López-Barrera et al. 2014, Muñiz-Castro et al. 2015). Species richness and floristic composition are affected by the effects of deforestation and fragmentation (e.g. Armenta-Montero et al. 2015; Lopez-Barrera et al. 2014; Meyer et al. 2016; Rueda-Hernandez et al. 2015; Gomez-Diaz et al., accepted). Therefore, the aim of this study is to describe land cover change and variations in forest spatial configuration in the highly diverse montane forest area of Central Veracruz since 1993 by 1) determining deforestation rates in the area throughout two periods (1993–2000 and 2000–2014), 2) classifying which are the old-growth forest types that have suffered the highest change rates, and 3) assessing the variations in the spatial patterns of forest cover over time by designated landscape metrics.

4.3 Methods

4.3.1 Study area

Our study area is located between 96°-97°W and 19°-20°N in the drainage basins of “La Antigua” and “Actopan” rivers. It covers approximately 6,987 km² located mainly in the central region of the state of Veracruz (Fig. 4.1), whereas a small fraction (ca. 7%) belongs to the state of Puebla. Our study area was chosen due to the outstanding species richness of angiosperms (6,876 species) representing about 31% of the Mexican flora (Luna-Vega & Espinosa 2013). A great portion of the state of Veracruz is located inside the Mesoamerican biodiversity hotspot, which is considered the sixth richest hotspot in the world (Myers *et al.* 2000, Mittermeier *et al.* 2005). Besides, the area has been identified as a center of biodiversity (Williams-Linera 2013) at the junction of the Neotropical and the Nearctic regions (Olson *et al.* 2001, Morrone 2005).

However, more than 80% of Veracruz’ primary vegetation has been converted and the remaining parts are highly fragmented (Muñoz-Villers & López-Blanco 2008). This area is therefore recognized as a priority region for conservation within Mexico (Williams-Linera 2002). The elevation of Central Veracruz ranges from 0 to 4,282 m, which turns it into a climatically and topographically varied area (Castellón *et al.* 2008), including several climatic zones (Lauer 1973) (Appendix 4.1). These are favored by numerous geographical factors, such as orography with elevation, distance to the Gulf of Mexico and continental air masses from the North (Delgado De Cantú 2003, Holwerda *et al.* 2010). The rainy season can be observed between May-June and September-October, (Lauer 1973), and a dry season between October and May (López-Barrera *et al.* 2014). The mean annual temperature gradient ranges from 2°C to 25°C, whereas the precipitation ranges from 600 mm to 2,000 mm per year; although the upper part of the mountainous area receives less than 500 mm of annual precipitation and in winter, above 3,400 m even snowfall is possible (Hietz & Hietz-Seifert 1995, Holwerda *et al.* 2010) (Appendix 4.1). The differences in climate, elevation, and the rock layer create extremely variable soil conditions (e.g. Muñoz-Villers *et al.* 2012) with the main soil types being calcic kastanozem, dystric folic andosol, eutric folic vitric andosol and eutric skeletal folic andosol (Bumiller 2015).

Along the altitudinal gradient, we found six vegetation belts: i) the tropical semi-deciduous forest (TSD), which is characterized by the trees *Brosimum alicastrum*, *Cedrela odorata*, *Bursera simaruba* and *Ficus obtusifolia* (Castillo-Campos & Travieso-Bello 2006), ii) the tropical oak forest (TOF) is typically dominated by one to three oak species (*Quercus oleoides*, *Q. laurina* and/or *Q. peduncularis*), whereas other tree species are scarce, iii) the humid montane forest (HMF) features frequent occurrences of fog as one of the most important characterizing ecological factors in this kind of forest (*bosque de niebla* or cloud forests) (Zamora-Crescencio & Castillo-Campos 1997), iv) the pine-oak forest (POF), which comprises a community whose dominant trees belong to the genera *Quercus* and *Pinus*, v) the pine forest (PF), which is dominated by several species of the genus *Pinus* (*P. montezumae*, *P. patula*, *P. pseudostrobus*, *P. teocote*) causing a high canopy openness, and vi) the fir forest (FF), which is a monospecific *Abies religiosa* community with sparse canopy openness. For a detailed description of the vegetation belts see Gómez-Díaz et al. (accepted).

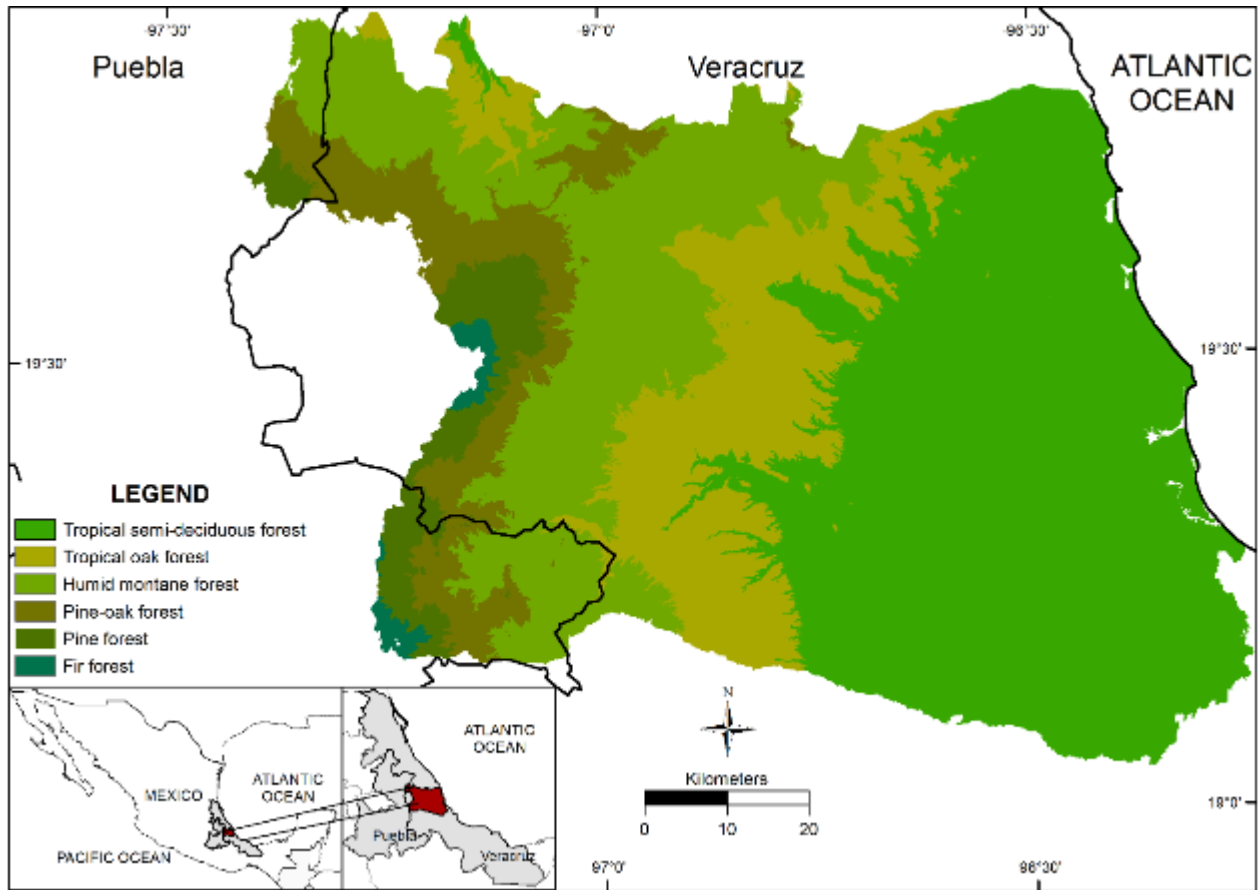


Figure 4.1 Study area in Central Veracruz, Mexico. Overview on the potential natural vegetation belts in the states of Veracruz and Puebla.

4.3.2 Land cover data

Historic land cover data for a period of 21 years, from the years 1993, 2000 and 2014 were obtained from image data of Landsat 5 TM, Landsat 7 ETM + and Landsat 8 OLI / TIRS, respectively. The scene selection was limited to the months of June to October in the rainy season, in order to be comparable with phenology or tree crown density in the partly deciduous forests. Due to the rainy season, there was an increased cloud cover within the selected scenes. Furthermore, due to the size and location of the study area, four Landsat scenes for each year were used to ensure full site coverage (Table 4.1).

Table 4.1 Overview of the Landsat satellite scenes used for forest change analysis and the most important information about the scenes (information refers to the total scene) taken from the metadata set.

Year	Sensor	Number of channels	Panchromatic channel (15 m resolution)	Date of recording	Scene (path/row)	Projection
1993	Landsat LT	7	-	04/09/1993	24/46	WGS84
	5 TM					UTM 15 N
	Landsat LT	7	-	04/09/1993	24/47	WGS84
	5 TM					UTM 14 N
	Landsat LT	7	-	26/08/1993	24/46	WGS84
	5 TM					UTM 14 N
Landsat LT	7	-	26/08/1993	24/47	WGS84	
5 TM					UTM 14 N	
2000	Landsat LT	7	-	23/09/2000	24/46	WGS84
	5 TM					UTM 15 N
	Landsat LT	7	-	23/09/2000	24/47	WGS84
	5 TM					UTM 14 N
	Landsat LE	8	Yes	06/09/2000	25/46	WGS84
	7 ETM					UTM 14 N
Landsat LE	8	Yes	06/09/2000	25/47	WGS84	
7 ETM					UTM 14 N	
2014	Landsat LC	11	Yes	13/08/2014	24/46	WGS84
	8 OLI TIRS					UTM 15 N
	Landsat LC	11	Yes	13/08/2014	24/47	WGS84
	8 OLI TIRS					UTM 14 N
	Landsat LC	11	Yes	19/07/2014	25/47	WGS84
	8 OLI TIRS					UTM 14 N
Landsat LC	11	Yes	19/07/2014	25/46	WGS84	
8 OLI TIRS					UTM 14 N	

Total belt area (TBA) was estimated based on previous studies conducted in the same study area by Carvajal-Hernández & Krömer (2015), Gómez-Díaz et al. (accepted) and Gómez-Díaz et al. (in revision).

4.3.3 Land-cover classification

We applied a supervised classification to level 1 Landsat data land cover types using maximum likelihood estimation (de Lange 2013). Therefore, training data for each mosaic dataset was created individually. For land cover classifications we tried to get at least 60 or 80 training pixels per land cover type. The land cover classes in the scenes of 1993 were interpreted largely visually. If uncertainties regarding forest or plantation inventory were detected, we used further vector data of 1997 with information about the vegetation types of Veracruz. The data are freely available for several decades on the server of the National Institute of Statistics, Geography and Statistics of Mexico (INEGI 2000). Another source was the classification for the upper drainage basin of “La Antigua” by Muñoz-Villers & López-Blanco (2008). Besides, there was a further classification made in 2003 (INEGI 2000), which was used for comparison and selection of appropriate training data of the scenes from 2000. Furthermore, we considered a classification from Ellis & Martínez (2010), for the total land cover of Veracruz.

The scenes from the year 2014 are only with ground truth data, i.e. vegetation surveys that have been mapped locally (Carvajal-Hernández & Krömer 2015). These vegetation surveys were based solely on different forest stands and have been raised in the course of a research project from 2012 to 2014. In order to facilitate the differentiation of difficult cover classes, we used the conditions detailed in Table 4.2.

Table 4.2 Description of the cover classes used for the land use classification.

Cover class	Description
Forest	We did not discriminate between primary and secondary forest due to the central satellite image resolution and quality scene differences from the period 1993-2014. Additionally, we were concerned in discriminating the forests with anthropogenic disturbance from the forests lacking such interference. Therefore, we considered a total of 140 (non-randomly distributed) ground control points available from previous field work in the study area and we used this GPS evidence to support the classification of different forest types.

Plantations	The plantation land cover class refers to fruit, vegetable and coffee plantations. Plantations are mostly recognizable for being parcelled, but also have a different land cover and different vegetation band color. In this case, coffee can only be classified as "plantation" if it is cultivated unshaded and/or as shaded monoculture because these kinds of plantations with few tree species may be differentiated from dense, high-growing tree stands to occur in the forest. Furthermore, disturbed surfaces as scrubby structures of pasture have been integrated into this class.
Other classes	In this category, we included the actual cloud surfaces and their shadows, water bodies, farmland, poor vegetation to vegetation-free areas as sand structured coastline and open rock formations in the mountainous area and coastal and hydro vegetation, which includes vegetation types that have been proven to be particularly adapted to the coasts (Leopold 1950).
Build-up areas	Under this category fell both residential and industrial areas, as well as paved roads. Suitable training data were cities like Xalapa at higher elevations, as well as José Cardel in the coastal lowlands.

4.3.4 Accuracy assessment

Before we conducted the land cover classifications for further analysis, we applied an Accuracy Assessment. According to Congalton (2004), we established a sample number of at least 50 training points per land cover class. To determine the classification accuracy of the reference pixels we created a confusion matrix with pixels of the grid.

The Producer's Accuracy is the percentage of reference points of a class, which was correctly classified within the grid and provides the classification information on the quality of its raster data. The calculation accuracy total serves to assess the quality of the raster data and to correct the possible classification problems in a given case, by revising the training areas (Congalton 2004).

The values obtained in the global accuracy, producer's accuracy, and user's accuracy measures, as well as the Kappa index, revealed the resulted accuracy assessment. The Kappa index was obtained with the Eq. (1) where π_0 is and the observational probability of agreement and π_e is a hypothetical expected probability of agreement under an

appropriate of baseline constraints such as total independence of observer classifications (Landis & Koch 1977).

$$\kappa = \frac{\pi_0 \pi_e}{1 - \pi_e} \quad \text{Eq. 1}$$

4.3.5 Deforestation for the diverse forest types and at area level

We counted together with the loss of original (gross) forest area ignoring zones of renewing or secondary forests and the net change in forest area in difference to other studies (e.g. Aide *et al.* 2013). We conducted two levels of deforestation analyses: i) the changes in the natural cover area were used to calculate the mean annual deforestation rates for each period (1993–2000; 2000–2014) at the regional level, and ii) the annual deforestation rates for the main old-growth forest types in the area were calculated. Both analyses were applied to the total area and on each vegetation type. The classification map for Veracruz proposed by Ellis & Martínez (2010) was used to obtain spatial information on vegetation belts. Then, we simplified the categories according to the classifications proposed by Carvajal-Hernández *et al.* (2015) and Gómez-Díaz *et al.* (accepted). We used the compound-interest-rate formula Eq. (2) proposed by Puyravaud (2003) to obtain annual net forest change and annual gross-forest rates. This formula has been used in similar studies (López-Barrera *et al.* 2014, Tapia-Armijos *et al.* 2015), where A1 and A2 are the area cover by natural forest at time t1 and t2, respectively and P is the annual deforestation rate.

$$P = \frac{100}{t_2 - t_1} \ln \frac{A_2}{A_1} \quad \text{Eq. 2}$$

4.3.6 Fragmentation analysis

In order to count and associate the spatial configuration of old-growth forest fragments, we used the landscape metrics proposed by Tapia-Armijos *et al.* (2015), taking into justification that the designated metrics were not redundant in the data achieved (Tapia-

Armijos *et al.* 2015). We used the program FRAGSTATS 4.2 (McGarigal *et al.* 2012) to calculate the following parameters as proposed by Tapia-Armijos *et al.* (2015): i) area of each individual patch (PA: Patch area); ii) the number of fragments of natural forest (NP: Number of patches); iii) the number of patches per km² (PD: Patch density); iv) the percentage of the landscape occupied by the largest fragment of natural forest (LPI: Largest patch index); v) the sum of the lengths (m) of all edge segments in the landscape, divided by the total landscape area in ha (ED: edge density); vi) the mean size of natural forest patches (MPS: mean patch size); vii) the total patch size remaining after removing a specific buffer edge (TCA: Total core area); and viii) the degree of isolation of natural forest patches resulting from measure the ratio between the size and proximity of all patches whose edges are within 1 km of the focal patch (MPI: Mean proximity index).

4.4 Results

4.4.1 Accuracy assessment

A confusion matrix was used for the corroboration of the land cover maps (Appendix 4.2). Our results showed an overall accuracy of 82.5% for the year 1993, 88.9% for the year 2000 and 84.3% for the year 2014, which means that the pixels with forest cover were correctly distinguished from those with other covers (plantations, other classes, and build-up) in the three years of land cover classification. For this study, the Kappa index was 0.81 for the year 1993, 0.88 for 2000 and 0.83 for 2014, which means that according to with Cook (2005), we had a good performance on the land cover classification for the three years (Appendix 4.2).

4.4.2 Deforestation and land cover change patterns

The land cover maps of 1993, 2000 and 2014 (Fig. 4.2) were used to derive variations in land cover (Table 4.3). Throughout the entire study period, the zone covered by old-growth vegetation was reduced by approximately 57%. For the first period (1993-2000) the annual net forest change rate in central Veracruz' extent was -0.44%; then in the second period (2000-2014) it increased significantly to +0.11%. For the whole study period (21

years) the mean net-forest change rate was -0.17%. Throughout the entire study period, the vegetation types that suffered the main conversion rates were fir forest and tropical oak forest (Fig. 4.3). For the first period (1993-2000), the annual gross forest loss rate was -1.17%, which was reduced significantly to -0.14% in the second period (2000-2014). Overall, tropical sub-deciduous forest and tropical oak forest were the vegetation types that suffered the highest gross forest loss (Fig. 4.3).

Table 4.3 Area covered by different natural forest types (FO), plantations, arable and grassland (AG) and other covers in 1993, 2000 and 2014 at different vegetation belts in Central Veracruz, Mexico. Total belt area (TBA) is also shown.

VEGETATION BELT	TBA	1993			2000			2014		
	(km ²)	FO	AG	Other	FO	AG	Other	FO	AG	Other
Tropical sub-deciduous forest (TSD)	3242	25%	69%	6%	21%	73%	5%	26%	68%	6%
Tropical oak forest (TOF)	1192	43%	56%	1%	29%	68%	3%	40%	53%	7%
Humid montane forest (HMF)	1595	54%	43%	3%	45%	48%	7%	51%	37%	12%
Pine-oak forest (POF)	604	44%	53%	3%	37%	57%	6%	47%	45%	8%
Pine forest (PF)	296	41%	51%	8%	31%	51%	19%	49%	41%	10%
Fir forest (FF)	58	36%	37%	27%	22%	43%	35%	34%	25%	40%

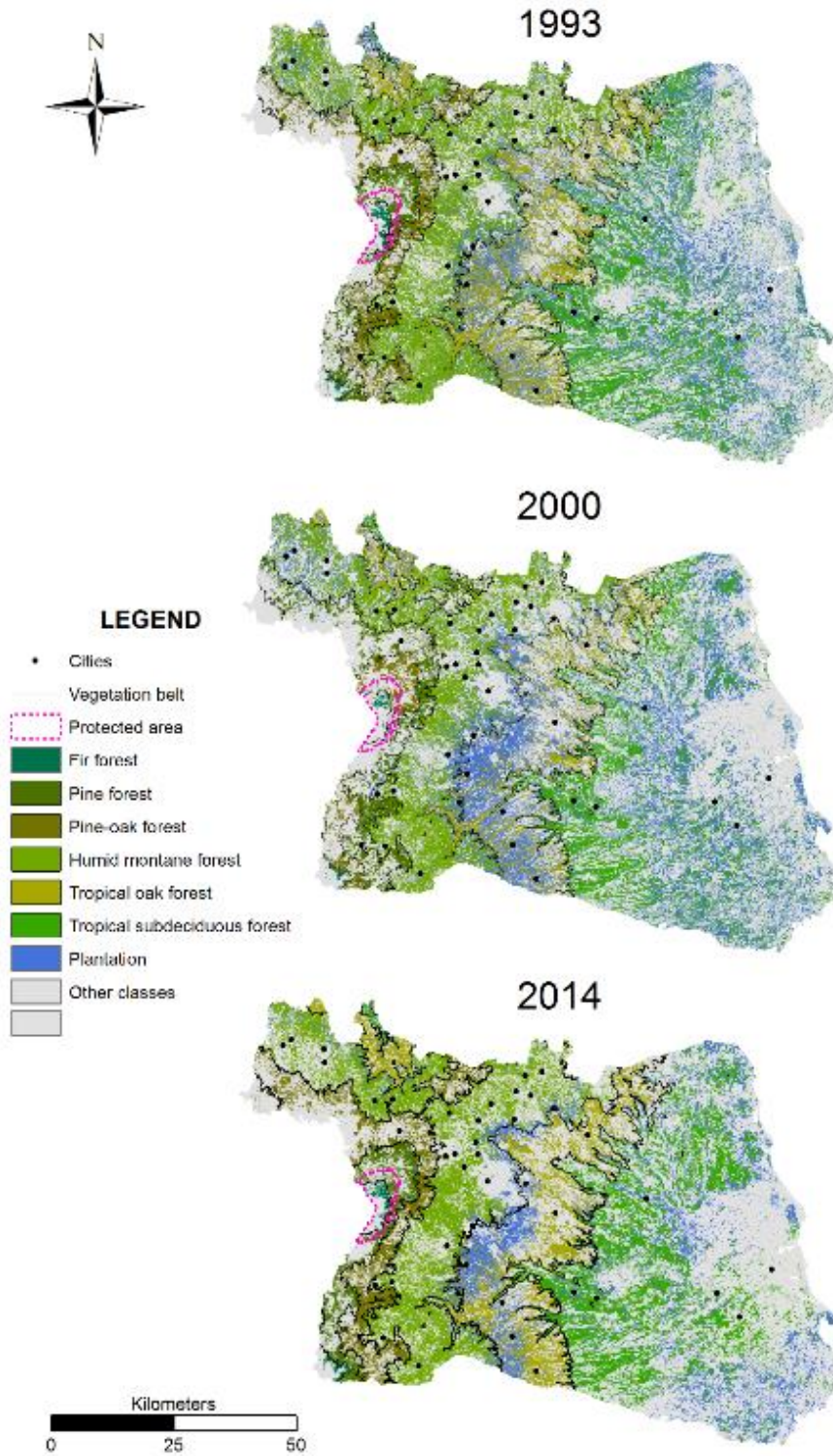


Figure 4.2 Land cover maps for the studied years (1993, 2000 and 2014). The spatial distribution patterns of the land cover types in Central Veracruz, Mexico is shown on the maps. The limits of the protected area are displayed in pink dashed polygons. The continuous lines show the border of each vegetation type.

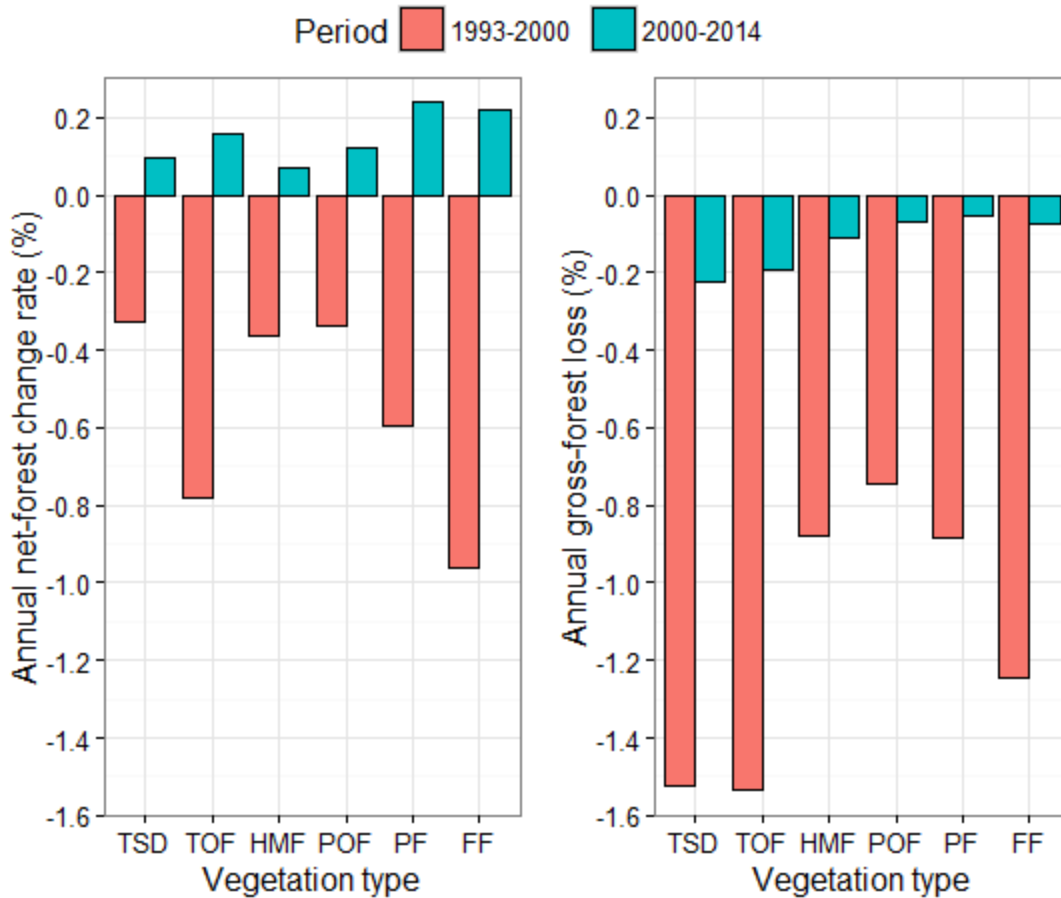


Figure 4.3 Annual net-forest change and gross forest loss rates (%) in four natural vegetation types in Central Veracruz, Mexico for the periods 1993-2000 and 2000-2013.

During the 21 years of the study period, 271 km² of the initial 2,586 km² of natural forest have been converted to plantations, another 592 km² has been transformed to grasslands, and additional 135 km² to non-natural covers. Tropical sub-deciduous forest and tropical oak forest were converted to plantations, grassland (68% and 53% of the initial area, respectively), and the fir forest and humid montane forest were converted to non-natural covers (40% and 12%, respectively) (Table 4.3).

4.4.3 Fragmentation patterns

The entire amount of forest patches increased from 76,983 to 100,831 in 2000 and decreased to 63,273 in 2014 demonstrating an 18% decrease in relation to the number of fragments existing in 1993 (Fig. 4.4 and Table 4.4). Mean forest fragment size increased from 0.03 km² in 1993 to 0.04 km² in 2014. The patch density decreased from 1,102 to 906 patches per 100km² (Table 4.4). The decreasing total edge length and the decreasing mean shape index value indicate decreasing irregularity in the shape of old-growth forest patches and a slightly decrease of vulnerability to edge effects. Considering a buffer region of 300 m, the entire core area of lasting old-growth forest increased by 573% from 1993 to 2014 to 18 km² today (Table 4.4).

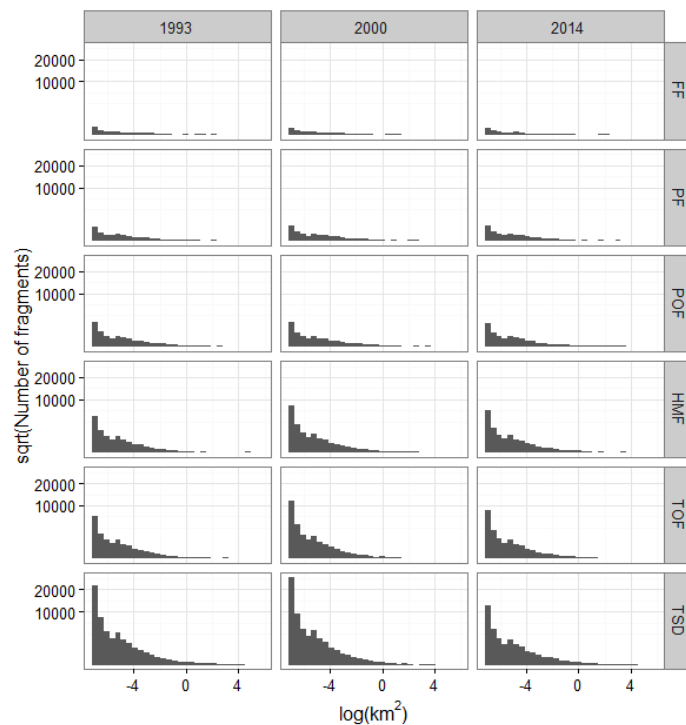


Figure 4.4 Variation of forest fragment size for 1993, 2000 and 2014 at the different vegetation belts (FF= fir forest, PF= pine forest, POF= pine-oak forest, HMF= humid montane forest, TOF= tropical oak forest, TSD= tropical sub-deciduous forest). The change in a number of forest fragments is displayed in the figure. The y-axis is the square root of the number of fragments and x-axis is the logarithmic area of the patches, we transformed the values in order to normalize the pattern and make it comparable.

Table 4.4 Variations in the spatial conformation of old-growth forests in Central Veracruz, Mexico throughout the period from 1993 to 2014. Metrics are: PA= total area of forest (km²), NP= number of patches, PD= patch density (number of patches/km²), LPI= largest patch index (%), ED= edge density (m/ha), AREA_MN= mean patch size (ha), TCA= total forest core area^a (km²) and PROX_MN= mean proximity index^b.

Forest	Year	PA	NP	PD	LPI	ED	AREA_MN	TCA	PROX_MN
FF	1993	21	494	24	40	245	4.16	0.00	263
	2000	13	463	36	28	310	2.77	0.00	125
	2014	20	397	20	41	238	4.99	0.01	404
PF	1993	121	1748	14	53	187	6.93	1.09	1598
	2000	91	2082	23	16	240	4.35	0.38	367
	2014	144	2144	15	34	186	6.74	3.06	1692
POF	1993	263	5310	20	15	258	4.96	0.20	946
	2000	223	4894	22	15	238	4.56	0.92	466
	2014	282	4839	17	14	218	5.82	2.03	973
HMF	1993	852	10872	13	30	306	7.84	0.02	14140
	2000	714	17013	24	24	282	4.19	0.79	3169
	2014	816	13767	17	29	245	5.93	2.99	7924
TOF	1993	510	14819	29	22	427	3.44	0.00	3950
	2000	348	24644	71	5	488	1.41	0.00	215
	2014	472	17466	37	13	319	2.70	1.38	1264
TSD	1993	815	47524	58	8	457	1.71	0.00	620
	2000	695	55517	80	8	481	1.25	0.00	320
	2014	836	28027	34	9	291	2.98	1.97	995

^a We measured a buffer region of 300 m length for the calculation of forest core area.

^b For the calculation of the mean proximity index, we considered a search radius of 300 m width.

In 2000, it happened that the mean proximity index was reduced due to the fact that the vicinity was less occupied by old-growth forest patches (Table 4.4).

4.4.4 Old-growth forest

We identified 1,100 km² of forest that had not been changed since 1993. These old-growth forests are located mostly at mid elevations in the transition of humid montane forest and pine-oak forest (Fig. 4.5 and 4.6). There are also small corridors in the tropical oak forest belt located at the ravines (Fig. 4.5 and 4.6). At the extremes of the altitudinal gradient, there are almost no patches of old-growth forest left (Fig. 4.5 and 4.6). The area of the regenerating forest after 2000 is 1,474 km², which represents 21% of the total study area and 57% of the forest area at 2014 (Fig. 4.2 and 4.6).

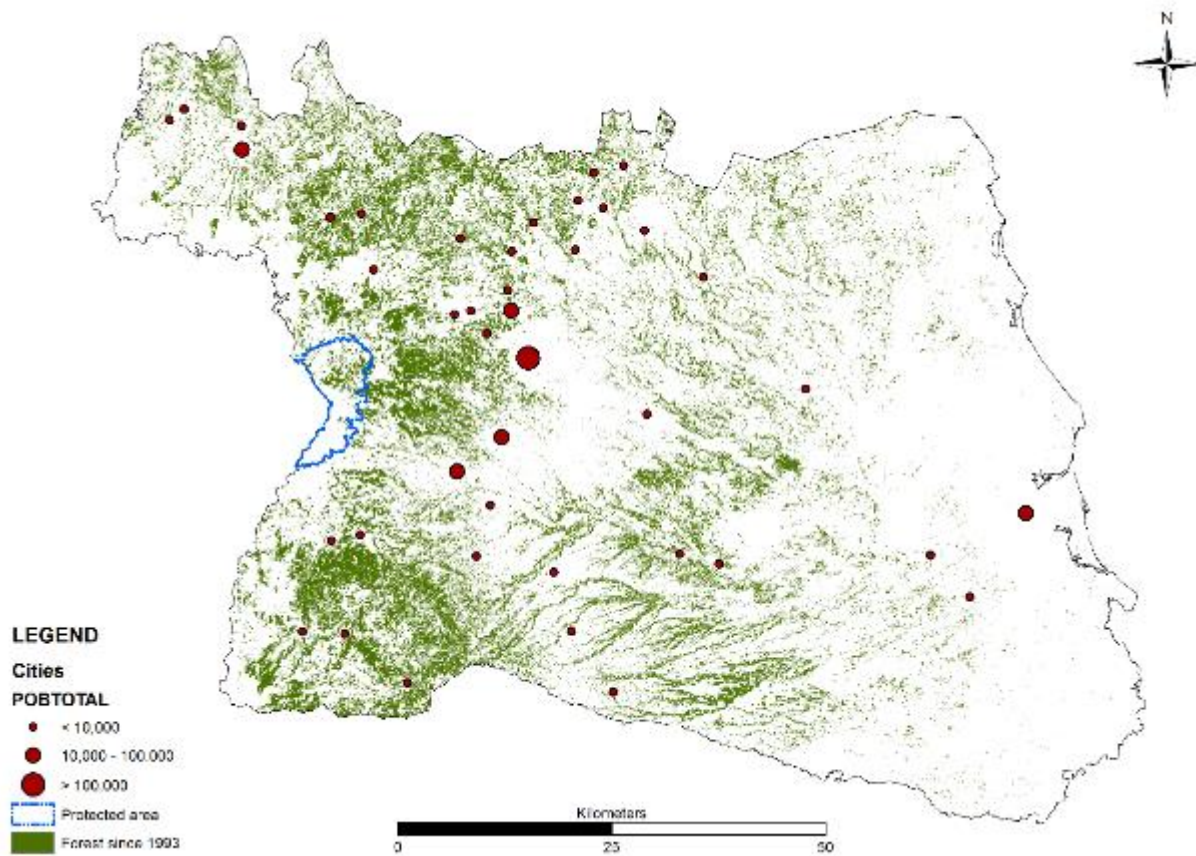


Figure 4.5 Sites with high conservation value. Fragments of forests without change since 1993.

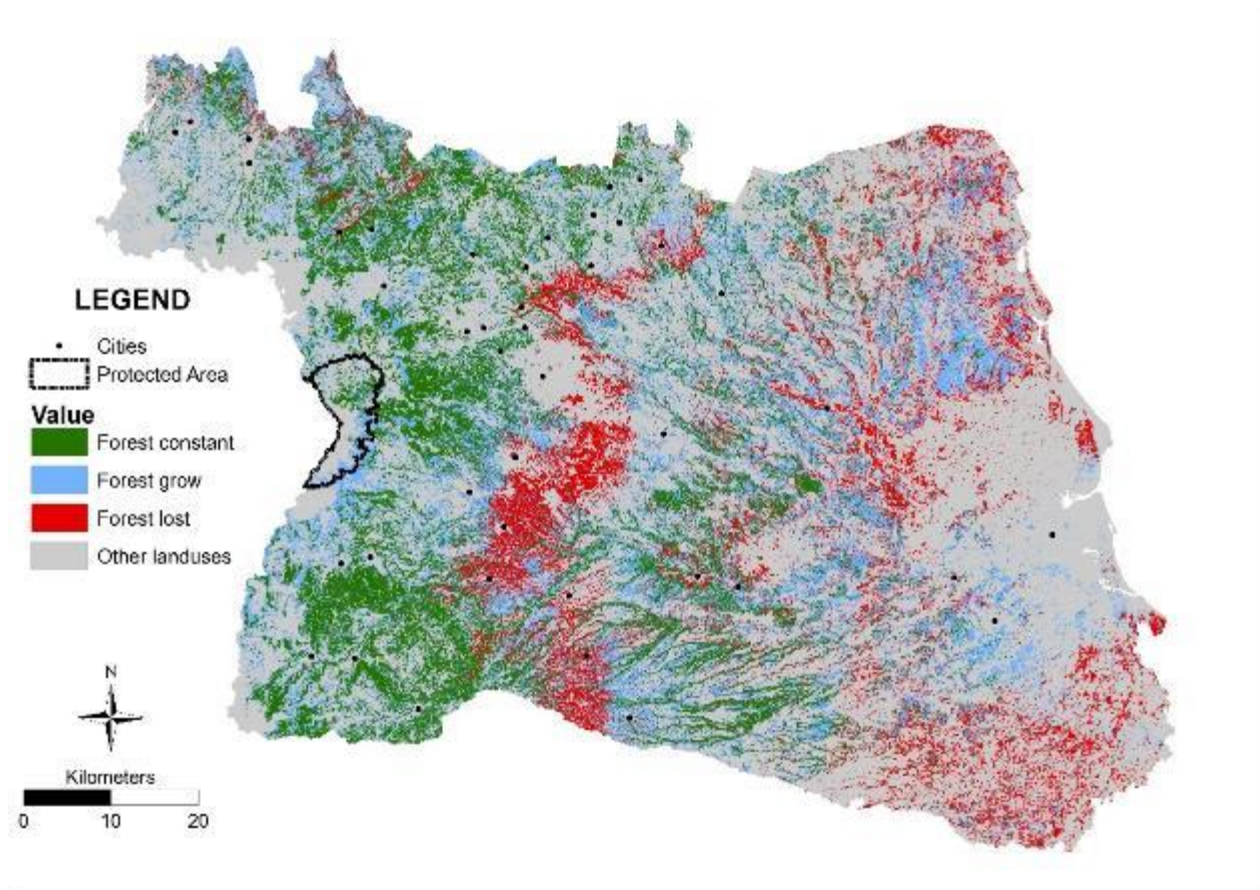


Figure 4.6 Change use analysis. Fragments of forests without change since 1993, forest grow since 1993 and forest loss since 1993.

4.5 Discussion

4.5.1 Deforestation patterns and fragmentation configurations

The old-growth forests of Central Veracruz have suffered high change rates throughout the most recent twenty years, although in the course of the most recent decade there is a reduction of this process. Throughout the period of 1993 to 2000, the annual net forest change rate (-0.44%) was lower compared to the one estimated for the whole country for the same period (-2.02%) (Masera *et al.* 1997) and even lower than the rate of Latin America (-2.5%) (Achard *et al.* 2002).

The public strategy on land uses of the Mexican government has an important contribution to the transformation of natural forest to other land uses. In the 1990s in Mexico, forest

deteriorations were related to the application of influential national motivations (e.g. PROCAMPO) by the Secretariat of Agriculture (SAGARPA) since 1994. These programs intended to encourage the establishment of livestock grasslands and agrarian parcels, which were causing the change of forest cover (Klepeis & Vance 2003). Another example is the forest loss and land degradation encouraged by the Idle Land Law (*Ley de tierras ociosas*) in the region of Los Tuxtlas, Southern Veracruz (Negrete-Yankelevich *et al.* 2013). For example, due to the arrival of different colonizers and probable parcel claims, local population could not leave any forest parcel unplanted. In consequence, important portions of forest cover were transformed to pastures and farmland throughout the 1960s and 1970s and unplanted wooded areas were changed. At national (Carabias *et al.* 2007) and state level (Gonzalez-Montagut 1999), similar arrangements of deforestation produced by legal reforms have been documented.

The accelerated destruction of the regional forest in Central Veracruz is a recent phenomenon. Data on territorial and population growth indicate that the explosion of urban growth soared from the 1960s. According to Marchal & Palma (1985), this growth was due to migration flows and Xalapa classified as a center of attraction of very high immigration. According to the INEGI (2000), the study area has been extensively used for agriculture and cattle. A substantial stress on old-growth forests is applied by the previous actions and the increase in human population, which has produced the decline of the lasting forests and the vanishing of vegetation cover (López-Barrera *et al.* 2014).

In addition to the overall reduction of forest area, we found that fragmentation patterns varied considerably between different time periods. In the first period from 1993 to 2000, the constant fragmentation of forest habitats was reflected in the reduction of the dimension of patches and the intensification in amount, irregularity, and isolation of forest patches. The growing isolation of old-growth forest patches due to the replacement by additional land cover types is a consequence of fragmentation. Gustafson and Parker (1994) suggested that a measure of the status of isolation is the mean proximity index. A rise in forest isolation, high amount of loss and degradation of forest extent and a reduction in entire core area was involved in this initial phase of fragmentation. Therefore, the preservation importance of the remaining forest fragments can be affected negatively due

to i) reduced plant-animal interactions (Tewksbury *et al.* 2002); ii) decays in vegetation and wildlife populations in remainder forest fragments (Laurance *et al.* 2002), and iii) reduced pollen movement and genetic diversity (Kwak *et al.* 1998).

The second period (2000-2014) experienced a slight recovery of forest (0.11%) (Fig. 6); similarly, (López-Barrera *et al.* 2014) reported an increase in forest cover (0.69%) in the period of 2000-2007 in Central Veracruz. Furthermore, there was an improvement in the connectivity of the landscape as several fragments that were isolated in the former period than were connected. One factor that can explain this recovery is the abandonment of agricultural land due to high rates of emigration (Tuirán 2002), which have recently accelerated in Veracruz State. The NAFTA free-trade arrangements were improved over the last decade (Pascual & Barbier 2007) augmenting rivalry from the US producers that led to reduced subventions for farming and livestock ranching coupled with the drop in international coffee prices (Hausermann & Eakin 2008) caused many farmers to abandon agrarian lifestyle in the study area.

In our study area, the deforestation and forest fragmentation are concentrated at the tropical semi-deciduous forest and tropical oak forest (Fig. 4.2 and 4.3), which are the vegetation belts at lowest elevations and with flat areas. These areas have been under human pressure since pre-Hispanic times (Sluyter & Siemens 1992). After the Spanish conquest, these areas were used for cattle and crops (Cortés *et al.* 2013). In the next centuries, they were extensively used to a degree that almost destroyed the original vegetation because of overexploitation and conversion to agricultural land (Gómez-Pompa & Castillo-Campos 2010). López-Barrera *et al.* (2014) explored the forest cover a few kilometers south of our study area, where they found that most deforestation happened more than a century ago and generalized rates of forest loss between 1973 vs. 2000 (-2.02%) and 1973 vs. 2007 (-0.59) were moderate to low. However, among different time periods, rates of forest loss varied significantly with minor reforestation (1.55%) during the period of 1973–1990, followed by a noticeable deterioration (-8.08%) in the period of 1990–2000, and lastly an obvious rise in forest cover (4.92%) in the period of 2000–2007 that matches with tendencies in population migration and modifications in public policy. They also found that the main factors that promote forest alteration were the

hydraulic infrastructure for yield irrigation, livestock grasslands and the nearness to mild hills.

4.5.2 Value of old-growth forests

It is important to distinguish between the value of the old-growth forest and secondary forests due to the ecological value of old-growth forests. In our study area, we found that deforestation has reduced the size of old-growth forests (Fig. 4.2 and 4.3). We found that the second period of our study (2000-2014) was characterized by a regrowth of new forests (Fig. 4.2 and 4.3) and an increase in the connectivity of the patches (Table 4.4). However, it is important to notice that those are young secondary forests, which are at most 14 years old and do not preserve the structure, biodiversity, and function of old-growth forests (Martin *et al.* 2013)).

According to Williams-Linera *et al.* (2016), there is a potential that secondary forest regrowth to old-growth forest in richness and diversity of trees in 15 and 25 years. Respectively, the average canopy height recovers after 35 years, and maximum height, basal area and density of trees after 80 years from clear cut logging. According to their results, active restoration suggests that the successional process on recently abandoned pastures and secondary forests (10 years), can be accelerated by the introduction of intermediate and late succession tree species.

There is only one formally protected area in our study area (National park “Cofre de Perote) that comprises only about 2% of the total surface (about 117 km², Fig. 4.2), and of this only 57% corresponds to core areas in which human activity is restricted (García-Romero *et al.* 2010). Besides, this park only protects two vegetation types (pine forest and fir forest), which are the vegetation belts with fewest species in our study area (Carvajal-Hernández & Krömer 2015; Gómez-Díaz *et al.* accepted) (Gómez-Díaz *et al.* in review).

According to the models of island biogeography (MacArthur & Wilson 1976), 50% of species can be lost only with a decrease to 10% of the original area. Therefore, preservation actions are an urgent task in the study area as indicate by our main results of forest gross loss. Furthermore, an extra issue to be considered is the extreme

fragmentation of these forests. The remaining original forest area would possibly constitute minor vegetation islands detached from each other (Fig. 4.5), a phenomenon that may have important consequences at the genetic, ecological and ecosystem functioning levels (Naeem *et al.* 2001). This condition is mainly perturbing since Veracruz is one of the most important states in Mexico regarding total plant species diversity and its flora is characterized by a high level of endemism (Gómez-Pompa *et al.* 2010, Villaseñor 2016).

According to Tschardtke *et al.* (2012), the capacity to re-organize an ecosystem service after disturbance is related to the landscape complexity. The species pool and the level of biological control is improved due to the increasing landscape complexity, as in the second period of our study (2000-2014), therefore after a disturbance, there is a rapid recovery in biological diversity. More species are maintained in complex landscapes, mostly due to the higher beta diversity, but also due to higher alpha diversity (Tschardtke *et al.* 2012).

Discriminating amongst the effects of habitat fragmentation versus degradation is an extra challenge in a landscape such as Central Veracruz since both processes may act together synergistically and often co-occur with adverse influences on the fauna and flora existing in fragments of natural vegetation. In this area, a high beta diversity among patches of the diverse forest has been detected (Gómez-Díaz *et al.* n.d., Carvajal-Hernández & Krömer 2015)(Gómez-Díaz *et al.* in review), which makes finding a reference forest for such comparisons particularly challenging.

Williams-Linera *et al.* (2007) proposed an enlargement of protected areas in Central Veracruz, especially where remnants of HMF old-growth forests can be found. Finally, on January 5, 2015, this area was decreed as a Natural Protected Area (ANP) under the category of Multifunctional Biological Corridor in seven fragments with environmental value, located in the municipalities of Xalapa, Banderilla, Coatepec, Emiliano Zapata and Tlalnelhuayocan (Gobierno del Estado de Veracruz 2015). The ANP is called "Archipelago of forests in the Capital Region of the State of Veracruz" and has seven fragments with a total area of 55.8 km². This archipelago reserve should promote the conservation and restoration of biological landscape corridors connecting forest fragments through riparian

forests, and biodiversity-friendly agricultural land, such as shade coffee plantations. Conservation has to be made compatible with sustainable economic activities and the preservation of the ecological environmental services that benefit the people living in the region.

4.6 Conclusions

In biologically diverse zones like Central Veracruz a better consciousness of the patterns, dynamics and spatial degree of forest fragmentation and deforestation is desirable. According to our study, this area demands an urgent attention on preservation initiatives because only 2% of the surface extent is below federal protection and 0.8% is under State protection due to the new reserve. It is important to protect the larger forest areas left in the pine-oak forest belt particularly as new construction plans will rapidly destroy the forest. The pressures to most of the studied environments are possibly even bigger than expected from our land use trajectory, for example through growing atmospheric nutrient deposition and upcoming climatic change.

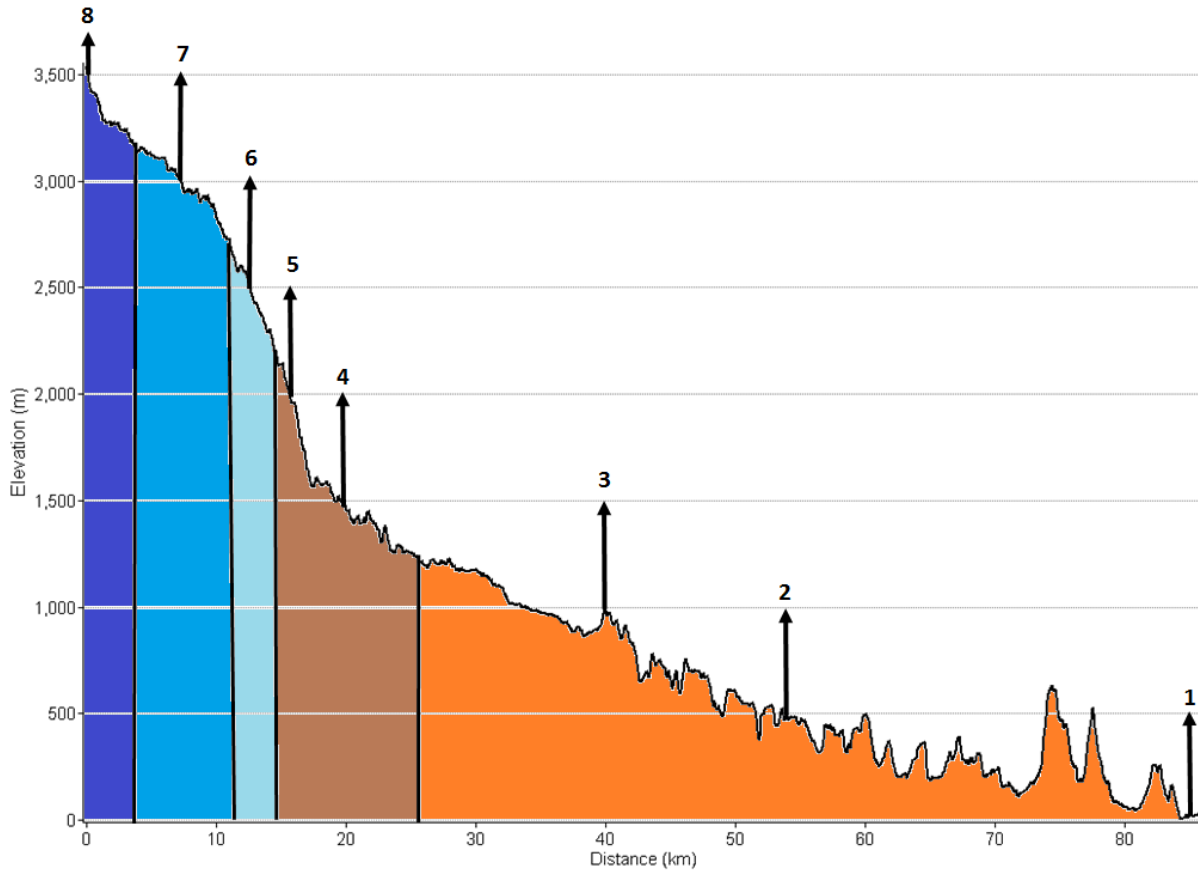
As an outlook, we can expect in the future for Veracruz a recovery and regrowth of some areas if the current deforestation rates continue. It is important to plan and design corridors that connect the old-growth forest with the young forest in order to promote the protection and development of biodiversity. It is important to preserve the young forest fragments because it takes at least 80 years to recover from disturbance. If special efforts will be done in protecting the forests of Central Veracruz it will take a lot of time on its cover will reach the same amount as 23 years ago.

4.7 Acknowledgments

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4.8 Appendix



Appendix 4.1 Elevational gradient. Study sites and climate zones according to Lauer (Lauer 1973) are shown (dark blue= “tierra helada”, blue= “tierra fria II”, light blue= “tierra fria I”, brown= “tierra templada” and orange= “tierra cálida”).

Appendix 4.2 Confusion matrix achieved from the accuracy assessment of the land cover map of Central Veracruz, Mexico. Other classes (arable, grassland, open country, coast and hydro).

Year	Classified	REFERENCE					User's accuracy (%)
		Forest	Plantations	Other classes	Build-up	Total	
1993	Forest	59	16	6	3	84	70.24
	Plantations	6	20	10	5	41	48.78
	Other classes	1	8	245	8	262	93.51
	Build-up	1	5	10	49	65	75.38
	Total	67	49	271	65	452	
	Producer's accuracy (%)	88.06	40.82	90.41	75.38		
	Overall accuracy	82.52					
2000	Forest	52	17	2	0	71	73.24
	Plantations	8	43	2	1	54	79.63
	Other classes	3	0	226	5	234	96.58
	Build-up	0	0	7	41	48	85.42
	Total	63	60	237	47	407	
	Producer's accuracy (%)	82.54	71.67	95.36	87.23		
	Overall accuracy	88.94					
2014	Forest	83	17	2	1	103	80.58
	Plantations	4	41	1	5	51	80.39
	Other classes	2	10	234	15	261	89.66
	Build-up	2	5	11	45	63	71.43
	Total	91	73	248	66	478	
	Producer's accuracy (%)	91.21	56.16	94.35	68.18		
	Overall accuracy	84.31					

CHAPTER 5: Synthesis



Echeveria rosea Lindl. in humid montane azonal forest in *El Encinal*, Acajete, Veracruz, Mexico.

5 Synthesis

At present, existing old-growth forests are becoming increasingly affected by forest use intensity and forest fragmentation. In order to investigate the effects that these pressures induce on herbaceous angiosperms, different vegetation types and habitats along an elevational gradient in Central Veracruz, Mexico were studied. Besides the influence of elevation, varying degrees of land use intensity were analysed, focusing on species richness, distribution and composition of herbaceous angiosperms (Chapter 2), their patterns of alpha, beta and gamma diversity (Chapter 3) as well as deforestation and fragmentation patterns of the different vegetation types (Chapter 4). Overall, this study pretends to contribute to the understanding of how forest use intensity affects a specific functional guild of plants and the old-growth forests in general.

5.1 Objective 1: Evaluation of distributional and diversity patterns of herbaceous angiosperms along an elevational gradient

In the area of the studied gradient, located in the tropical zone of Mexico, we found a moderate diversity of herbaceous angiosperms (Chapter 2), as the 264 reported species represent 5.7% of species of Veracruz' herbaceous angiosperm flora and about 1.8% of Mexico (Villaseñor 2003, 2004, 2016, Espejo-Serna *et al.* 2004, Villaseñor *et al.* 2007, Villaseñor & Ortíz 2014). This species richness is considered as moderate because the sampled area represents only 0.0001% of the total area of the state of Veracruz. The observed species richness, including endemic elements, highlights the importance of the area for plant conservation and shows the need to continue with floristic studies in order to actualize and complete the inventories of the existing biodiversity in specific regions (Magaña & Villaseñor 2002).

The elevational sites with highest species richness of herbaceous angiosperms were 2,500 m (76) and 1,500 m (52), which is a diversity pattern similar to other elevational gradients realized in other latitudes of the Neotropics, where the highest diversity was found at mid-elevations (Vázquez & Givnish 1998, Nogués-Bravo *et al.* 2008).

The climate gradient along the elevational gradient also shows the registered pattern of these studies, with a linear decrease in the temperature as the elevation increases. In the case of light intensity, this increases with elevation due to is more intense solar radiation in the higher areas (Carvajal-Hernández 2016). However, in this gradient, the mean annual temperature values are different compared with other zones of the Neotropics (Lippok *et al.* 2014), with lower values at the high areas of the gradient due to snow in winter and higher values in the lowlands due to prolonged drought periods. The harsh climatic conditions at the extremes of the studied gradient are considered as limiting factors for many species, which entails to a lower diversity.

The highest species richness was concentrated at higher elevations (2500-3000 m), which corresponds to the distribution area of the pine-oak forest and pine forest, while the number of species decreases at the extremes in more than 80% (Chapter 2). A hump-shaped pattern has been found in different groups of vascular plants along tropical elevational gradients, such as ferns (Salazar *et al.* 2015), terrestrial herbs (Willinghöfer *et al.* 2011) and shrubs (Chawla *et al.* 2008). In our study, the highest species richness was found at 2,500 m, which has been also reported from Ecuador for all endemic vascular plant species, endemic species of Acanthaceae, Asteraceae, Lamiaceae, Piperaceae and Scrophulariaceae (Kessler 2002), and for liverworts in the Northern Andes (Wolf 1993). However, our results show differences in previous findings as the peak in species richness shifted towards higher, instead of mid-elevations (Kluge & Kessler 2006). The concentration of species richness in this area corresponds to the record of moderate temperatures and high environmental humidity, which have been shown to favor the establishment of herbaceous angiosperms (Hawkins *et al.* 2011). Notably, the species richness recorded in azonal vegetation (ravines or riparian vegetation), was higher than in old-growth forest in two elevational belts, which indicates that these specific areas are important reservoirs of herbaceous angiosperms diversity.

Due to the large elevational range of the study gradient, it was not possible to compare it completely with similar works realized with herbs in Mexico. However, when comparing it by sections, it was observed that the richness we found was lower (Vazquez *et al.* 1995, Vázquez & Givnish 1998, Castillo-Campos *et al.* 2007, García-Franco *et al.* 2008),

coincident (Encina-Domínguez *et al.* 2007) or even higher (Krömer *et al.* 2013, Palacios-Wassenaar *et al.* 2014). When comparing the richness of our study with other regions near to the Equator, our study area has lower values than in those areas. Thus, it is corroborated that the diversity of herbs decreases slightly along a latitudinal gradient from the Equator to the poles (Hawkins *et al.* 2011), as for example the tropical area in Mexico.

5.2 Objective 2: Evaluation of forest use intensity effect on the patterns of richness and composition of herb species

The forest use intensity does not affect the species richness of herbaceous angiosperms in a direct way since there was no loss of herb diversity caused by land use change. However, it affects the floristic composition (Chapter 3). Though, the degree of community affectation does not occur equally along the altitudinal gradient and also depends on the intensity of the forest use. For example, at low and high elevations there is a slight increase in alpha diversity of herbs due to the effect of forest use intensity, whereas the opposite happens at mid elevations. It is interesting to note that at both extremes of the gradient (50 and 3500 m), there is no shift on alpha diversity between habitats.

The lack of a detectable net-change in alpha diversity might indicate that the level of forest use intensity is still moderate and that herbs are better adapted to changes in the environment with a profit from better light conditions in degraded or secondary habitats. The Asteraceae and Poaceae were the families with the greatest increase in species richness in relation to land use intensity, consequently, it has been demonstrated that they are adapted to high light incidence and drought (De Moraes *et al.* 2016).

In terms of beta diversity, the middle part of the elevational gradient presented the highest species turnover (with replacement rates ranging from 60% to 78% according to the Sørensen index) (Fig. 3.4); thus, this area requires special attention for its conservation. The values of beta diversity are higher when a forest habitat is transformed into another one than within the same forest. The species composition is highly modified when the old-growth forests are transformed into secondary forests, especially at mid-elevations. This is because forest degradation causes a higher heterogeneity of environmental conditions

(Warren *et al.* 2007), which leads to higher competition between species adapted to disturbance and old-growth forest species (Schultz & Dibble 2012).

The values of alpha and beta diversity present along the land use intensity gradient are related with conditions in the microclimate. Carvajal-Hernández (2016) corroborated in the same plots that when there is an anthropogenic disturbance, the clearings in the canopy and the radiation towards the interior of the undergrowth increase. This situation influences directly the microclimatic conditions, observing an increase in the incidence of light and temperature, as well as a decrease in relative humidity (Scatena *et al.* 2005). In general terms, there is an increase of 0.6°C in mean daily temperature (Carvajal-Hernández 2016), which might be related to a high turnover of species (Chapter 3). These changes are more notable in the vegetation types located at mid-elevations of the gradient (humid montane forest and pine-oak forest). Such situation is alarming due to the fact that those areas along the elevational gradient are under high anthropogenic pressure (CONABIO 2010). Also, there we found two endemic species to Veracruz, which corroborates the marked specificity of conditions that require most of the sensitive species of herbaceous angiosperms (Chapter 3).

5.3 Objective 3: Analysis of the current conservation status of forest fragments in the study area

The analysis of deforestation in Central Veracruz, Mexico revealed that almost 57% of the original natural cover disappeared since 1993 at an annual deforestation rate of -0.44% for the period of 1993-2000 followed by a reforestation rate of 0.11% for the period of 2000-2014, showing a marked or slight decrease of deforestation during the last fourteen years. However, when it was considered the annual gross forest loss rate the perspective changes because in the first period the rate was -1.17% and in the second period, the rate was reduced to -0.14% (Chapter 4). Even with this decrease in the deforestation and gross forest loss rates, Central Veracruz has actually one of the highest deforestation rates in Mexico together with the seasonal tropical forests of Southern Yucatán (Ramírez-Delgado *et al.* 2014), *Selva Maya* region (Simbangala & Cámara 2016) and *Sierra Madre de Chiapas* (Cortina-Villar *et al.* 2012). In the study area, the deforestation is mainly

concentrated at low elevations where tropical semi-deciduous forest and tropical oak forest are the two vegetation types that exhibit the highest rates of conversion. Most of the human settlements and productive activities on the Eastern slopes of *Cofre de Perote* are located in the tropical semi-deciduous forest and humid montane forest close to main rivers and roads, indicating that accessibility is one of the main drivers of deforestation in this zone. In the case of a tropical oak forest, which is mainly located in the humid and warm valleys, the patterns of deforestation are more diffuse because major agricultural activities date back to the colonial era. Although, the rates of deforestation of the humid montane forest and pine-oak forest are less important compared with the other vegetation types, about 1% of their area disappeared every year since 1993. This is important to emphasize because the largest well-preserved remnants of humid montane forest and pine-oak forest in the state are located in Central Veracruz (Gillespie *et al.* 2012). Here, the forests are being degraded and converted to pastures which are common all over the country but particularly in this region most soils are of low fertility. These pastures are not very productive with the consequence that the remaining forest is being cleared progressively (Poore 2013).

Like deforestation, the fragmentation process has also reduced in the region where the number of forest fragments has decreased by 18% compared with the number of fragments registered in 1993, although it is still a high number of small fragments (63,273). Actually, the regional landscape is characterized by few large fragments most of which are without protection and many patches of less than 1 km². Additionally to the decrease of forest patch size, it was also observed that separation grows between patches by 15% and a decrease in the regularity of patch shapes (Chapter 4). The current composition and configuration of Central Veracruz' landscape could have a direct influence on its ecological functionality jeopardizing the availability of viable populations, species richness and the high biodiversity that characterizes this area (Fahrig 2003).

Both processes, deforestation, and fragmentation are the results of human pressure on natural habitats. In Central Veracruz, the levels of human pressure have increased since 1993, but the increase is more noticeable in the mid- and low elevations. This is because at mid-elevations are located some localities that were least accessible and populated

areas until the late 1960s when the government constructed several connecting roads and highways. Since then, human density and human activities have increased in this area. Despite this, it still has some of the largest forest fragments without modification since 1993, especially on the Southwestern slopes of *Cofre de Perote* at the border with the state of Puebla (Chapter 4).

An important finding of this investigation is how human impact differentially influences the natural vegetation types. For example, forest cover was mainly transformed into arable and grassland in all vegetation types with the exception of fir forest, where the forest was mainly transformed into no vegetation. As mentioned by Ellis & Ramankutty (2008) it is essential to propose more effective conservation plans to recognize the different patterns and drivers that promote transformation.

5.4 Overall conclusions

The current study demonstrates that alpha diversity of herbaceous angiosperms does not necessarily decrease with increasing forest use intensity (Chapter 3). However, values of beta diversity show that there is a high species turnover due to forest use intensity.

In terms of diversity along the elevational gradient, we found high values of beta diversity (which indicates a high environmental heterogeneity) when different elevations were compared, even if these are contiguous or even if they share the same vegetation type (Chapter 3). This situation highlights the vulnerability of herbaceous angiosperms adapted to old-growth forests and requires to reconsider the conservation efforts in the study area. It is preferable to focus the efforts in preserve heterogeneous systems that include a mosaic of different vegetation types (Chapter 4). The high number of species adapted to azonal areas (ravines and riparian forests) highlights also the importance of this vegetation type as a reservoir of native herbaceous angiosperms. Therefore, the conservation of fragments of those environments in Central Veracruz should be considered in future conservation plans (Chapter 2).

As in the mid-elevation ecosystems is concentrated the highest diversity of species and in those environments, the climatic contrast caused by the anthropogenic disturbance is

more accentuated, which is an indication that these are the most vulnerable ecosystems for the conservation of native herbaceous angiosperms. Similarly, most of the natural forests present along the studied elevational gradient are at risk of disappearing due to the existing anthropogenic pressures (Chapter 4).

The results and findings described in the different chapters of this dissertation add new information related to the poor knowledge on herbaceous angiosperms along gradients of elevation and land use intensity so far available for Mexico, especially for Veracruz. However, additional studies are needed to understand better how the environmental conditions or territorial dynamics influence the persistence of herbaceous angiosperms in the long term. For example, we need to understand which abiotic factors (e.g. microclimate or soil) are influencing the observed diversity patterns, also how the highly fragmented landscape in Central Veracruz is influencing the population dynamics of native herb species. Here we describe the patterns of alpha, beta, and gamma diversity, but it is necessary to generate more information about the factors that are affecting each of these patterns.

There is information about factors (e.g. paedogenesis, latitude, nutrient availability) that promote alpha diversity in many other taxa (e.g. trees, herbivores, soil microbes) but information about factors promoting alpha or beta diversity of herbs is still insufficient. Besides, more research about the concordance of alpha and beta diversity patterns in different taxa would be helpful to understand the potential of using biodiversity surrogates (e.g. endemic plant species).

It is important to remark that a lot of data on soil properties, microclimatic and spatial information has been generated, which is going to be used in further analyses:

- To understand how soil and microclimate influence the patterns of alpha and beta diversity of herbaceous angiosperms along the elevational gradient.
- To create species distribution models in order to understand how climate change is going to influence the patterns of alpha and beta diversity.
- To describe the immediate and underlying causes of deforestation.



Deforestation for charcoal production at the humid montane forest in *Los Capulines*, Tlaxnelhuayocan, Mexico at 1500 m.

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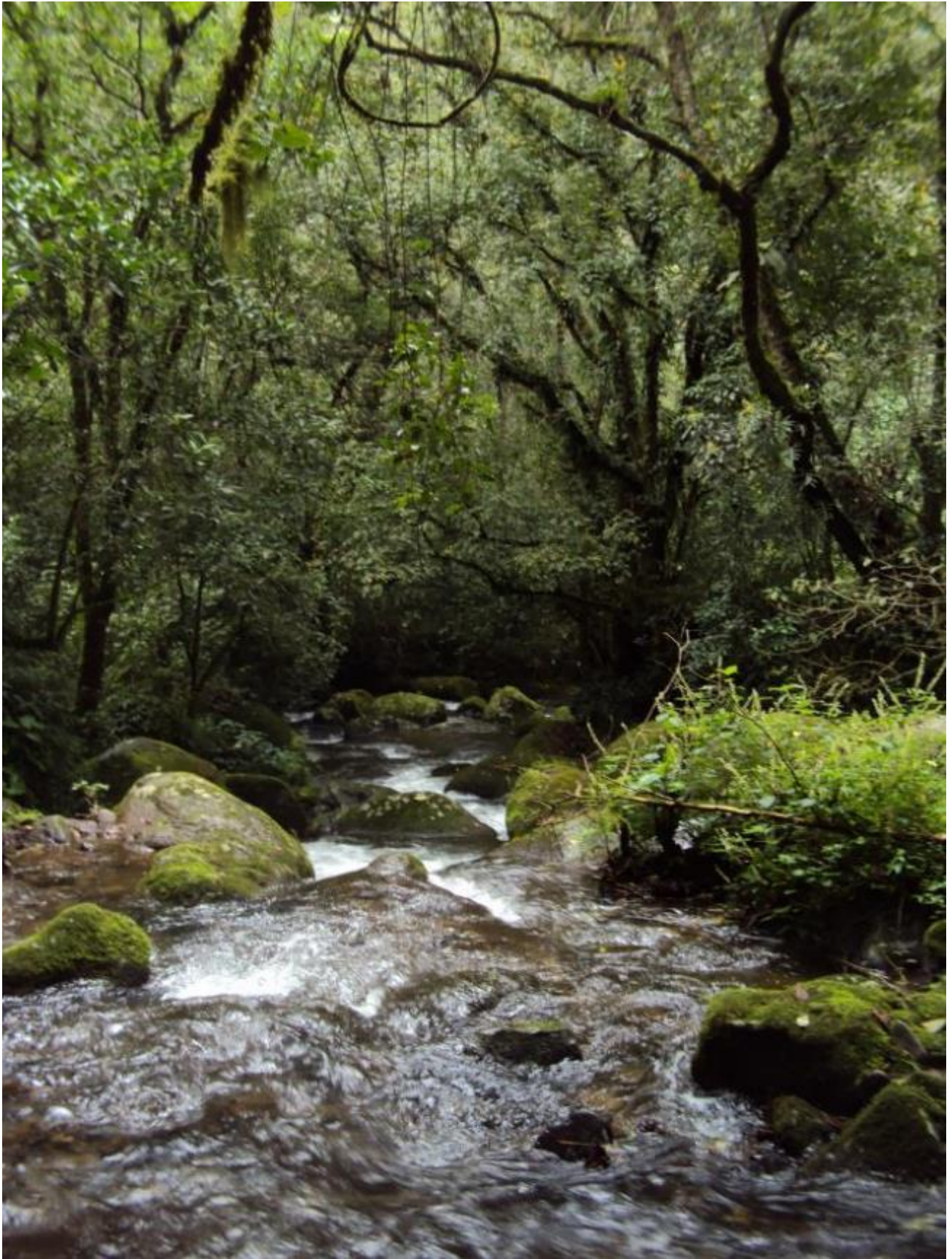
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EDUCATION

- 2012 – Jan. 2017 University of Göttingen. Department of Physical Geography
Research. Dr. candidate
- Jun. 2012 Especialist in Statistical Methods graduation.
- 2011 – 2012 Universidad Veracruzana (UV), Xalapa, Veracruz, Mexico.
Faculty of Statistics and Informatics, School of Statistical Sciences.
- Oct. 2010 *Licenciatura* in Biological Sciences graduation (equivalent to Diplom).
- 2006 – 2010 Universidad Veracruzana (UV), Xalapa, Veracruz, Mexico.
Faculty of Biology.
- 2003 – 2006 “Colegio preparatio de Xalapa” High school. Xalapa, Mexico.

LANGUAGES

- Spanish Native competence.
- English Full professional competence.
- German Basic professional competence.

EXPERIENCE

- 2012 – present **Dr. rer. nat. Studies.** Research student in BIOVERA project sponsor by CONACYT, DAAD, DFG in Mexico.

- 2011 – 2012 **Research assistant.** Centro de Investigaciones Tropicales (CITRO), Universidad Veracruzana (UV). Fieldwork and herbarium assistant in several projects in Mexico.
- 2011 – 2012 **Ecotourism guide.** “Huella” Club, Xalapa, Mexico.

OTHER RELEVANT EXPERIENCE

- 2012 **Research Scholar.** School of Statistical Sciences, Universidad de Costa Rica (UCR), San José, Costa Rica.
- 2010 **Research Scholar.** El Colegio de la Frontera Sur, Campeche, Mexico.
- 2009 **Research Scholar.** Center of Biological Sciences, Universidad de Guadalajara (UDG), Guadalajara, Mexico.

PRESENTATIONS

- Feb. 2016 Species richness and distribution of herbaceous angiosperms along gradients of elevation and human disturbance in Central Veracruz, Mexico. Annual Conference of the Society for Tropical Ecology (GTÖ), Göttingen, Germany. Oral presentation.
- Sep. 2015 Species richness and complementarity of herbaceous angiosperms along an elevational gradient in Central Veracruz, Mexico. The annual meeting of the German Society of Ecology, Göttingen, Germany. Poster.
- Apr. 2015 Species richness and complementarity of herbaceous angiosperms along an elevational gradient in central Veracruz, Mexico. Annual Conference of the Society for Tropical Ecology, Zurich, Switzerland. Poster.

- Oct. 2014 Influence of altitude and human impacts on diversity of ferns and herbs and soil parameters at the “Cofre de Perote” (Veracruz, Mexico). 11th Latin-American Botanical Congress. Salvador da Bahia, Brazil. Poster.
- Feb. 2014 Herbaceous angiosperms along elevational and disturbance gradients in central Veracruz, Mexico. Annual Conference of the Society for Tropical Ecology. “Tropical Ecosystems – Between Protection and Production”, at the Ludwig Maximilian University of Munich, Freising in February. Oral presentation.
- Nov. 2013 Influence of altitude and human impacts on diversity of ferns and herbs and soil parameters at the “Cofre de Perote” (Veracruz, Mexico). Symposium on Interdisciplinary project Cofre de Perote, at the Centro de Investigaciones Tropicales (CITRO), Xalapa, Mexico in November.
- Jul. 2013 Herbaceous ferns and angiosperms as indicators of soil parameters along an altitudinal gradient at the “Cofre de Perote” (Veracruz, Mexico). XI Symposium of Mexican students and studies in the UK. Sheffield, United Kingdom. 11-13 July. Oral presentation.
- Dec. 2012 Herbaceous ferns and angiosperms as indicators of soil quality and microclimate along an altitudinal gradient in the central gulf of Mexico. Latin America Symposium, Neotropic-Challenges for Integrative Ecology. Bonn, Germany. 17-18 December. Oral presentation.
- Nov. 2012 Efectos altitudinales, antropológicos y ambientales sobre patrones ecológicos de helechos y angiospermas herbáceas. 2° Grantees and former grantees Symposium CONACyT in Europe. Strasburg, France. 29-30 November. Oral presentation.

AWARDS

CONACYT – DAAD Scholarship 2012-2016. Consejonacional de ciencia y tecnología (Mexico) and Deutscher Akademischer Austausch Dienst.