

Maintenance mechanisms of tree diversity in Mexican coniferous forests

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Abstract

This project aims to understand how the diversity of conifers in Mexico been generated and the mechanisms through which it is maintained. Specifically I ask how conifer diversity is influenced by environmental drivers, how the distribution of conifers in Mexico is influenced by environmental stressors and the extent to which the traits exhibit phylogenetic conservatism and how beta diversity patterns are shaped by geographic and environmental distance. In order to answer this questions I used data from the Forest and Soils National Inventory of the Mexican Forestry Commission, a database of conifer traits, environmental data and a phylogeny of Mexican conifers. The results show that environmental variables influence species richness and functional diversity to varying extents. There was however a consistent effect of the interaction of temperature and precipitation on both species richness and functional diversity. I found that temperature and precipitation seasonality do not necessarily constrain species richness or functional diversity. Annual precipitation was showed to be the environmental variable that best explains the geographical patterns of conifer traits in Mexico. Overall, the functional traits exhibited phylogenetic signal consistent with niche conservatism, with several functional traits showing dependency with climate variables even after correcting for phylogenetic relatedness. Beta diversity across Mexico is mostly influenced by environmental distance. However, both geographic and environmental distance play important roles in shaping species, functional and phylogenetic beta diversities.

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Chapter 1

Introduction

1.1 Origins and maintenance of tree biodiversity

What is Biodiversity?

Biodiversity can be broadly defined as the sum total of all the biotic variation across Earth from genes to ecosystems (Purvis and Hector, 2000; Dirzo and Raven, 2003). Biodiversity is heterogeneously distributed across the planet and the variation in its patterns can be described through a number of approaches, for example, with patterns in biodiversity hotspots, diversity variation across spatial scales and with environmental and spatial gradients (Gaston, 2000). Several factors such as climate, history of the taxa, paleogeography and a range of abiotic factors influence the patterns of biodiversity (Barthlott et al., 1996).

The majority of studies that assess biodiversity patterns and its drivers take a taxonomic diversity approach, and although most of the advances in the understanding of diversity patterns have been made through this approach, the incorporation of functional and phylogenetic components of biodiversity is needed for a more comprehensive understanding of biodiversity (Swenson, 2011a; Munguía-Rosas et al., 2014). It is a concept influenced by variables such as different time and spatial scales, and where conflicting taxonomic, trait and phylogenetic diversity patterns are common (Pavoine and Bonsall, 2011).

Species richness is often used to describe diversity at taxonomic or species level (Pavoine and Bonsall, 2011). Measuring taxonomic diversity with an index such as species richness where all species are treated equally, as evolutionary and ecologically equivalent and independent, and providing little insight into the functional roles and evolutionary history of species, is a

limitation to an accurate assessment of the drivers of diversity patterns (Swenson, 2011b; Chun and Lee, 2017).

Functional diversity is the value and range of functional traits of the species present in a determined ecosystem (Dıaz and Cabido, 2001). Value means the presence or abundance of a certain trait and range means the difference between the extreme values of a trait (Dıaz and Cabido, 2001). It is an important component of biodiversity, as it addresses community and ecosystem ecological questions based on the organism's role (Petchey and Gaston, 2006). A trait is a measurable property of a species that can be measured at the individual level and used comparatively across species. A functional trait is a trait that is relevant to a species' performance in its environment (McGill et al., 2006). Functional diversity is calculated by measuring functional trait diversity, which is the variation of traits between organisms and can be accomplished by calculating a number of functional diversity indices, depending on the type of traits and the application of the functional index (Carmona et al., 2016; Laliberte et al., 2010; Petchey and Gaston, 2006). Functional diversity has been used as an approach to ecological questions such as to explain environmental and spatial gradients (Swenson et al., 2012) and for the understanding of ecosystem services, which are the benefits provided by ecosystem processes to humans, and the potential risks ecosystems face from environmental change (Díaz et al., 2013).

Phylogenetic diversity is a measure of the diversity of lineages in a species assemblage (Faith, 1992). As with the rest of the diversity components, there are several metrics for quantifying phylogenetic diversity that can be grouped in two different types. Type I metrics start by calculating an index of evolutionary distinctness, which is the distance along the phylogenetic

tree from one species to its nearest relative, such as taxonomic distinctness, species originality or species evolutionary history for all species in a regional phylogeny and then calculating the sum of these indices for subsets of species in that particular phylogeny (Vellend et al., 2010). Type II metrics start with a regional phylogeny. However the phylogenetic diversity measure of a species subset in a regional phylogeny depends just on the properties of that particular subset. Examples of these measures are phylogenetic diversity, mean phylogenetic distance and mean nearest neighbour distance (Vellend et al., 2010). The choice of metric greatly depends on the type of phylogenetic data available and if the species data are presence/absence, or if abundance data are available (Vellend et al., 2010). A measure of phylogenetic diversity indicates a measure of current and future biodiversity and ecosystem services derived from evolutionary processes, given that the greater evolutionary history represented, the more ecosystem services will be provided by a set of taxa. This is under the assumption that phylogenetic diversity is an indicator of feature diversity as species characteristics or traits (Faith, 1992; Faith et al., 2010).

Scales of diversity

An important aspect for understanding the distribution and how species are generated and maintained is the spatial scale on which they are quantified. Diversity can be partitioned into alpha (α), beta (β), and gamma (γ) components (Whittaker, 1960). The processes that influence diversity patterns vary at different scales, from density-dependent processes such as herbivory and competition at local scales, to environmental filtering of species by biotic and abiotic factors at a broader scale, and historic and biogeographical processes like extinction and speciation at regional scale (Cavender-Bares et al., 2009).

Local coexistence (alpha diversity)

Alpha diversity refers to the diversity components (taxonomic, functional and phylogenetic diversity) present within a local community or assemblage (Graham and Fine, 2008; Arnan et al., 2017). Alpha diversity measures can be classified into two groups, in 1) sampled or estimated species richness such as species accumulation curves, and 2) in species abundance distribution, using indices such as Simpson or Shannon-Weaver (Jurasinski et al., 2009). Hill numbers, also called effective number of species, which means the number of equally abundant species required to give the same value of a diversity measure, are a family of diversity indices that differ only by a parameter q that incorporates species richness and relative abundances (Chao et al., 2014a). Hill numbers have recently gained popularity given the advantages they present over other indices. The most important one is the replication principle that states that if two equally diverse assemblages have no species in common, then the diversity will double if the two assemblages are combined. Another advantage is that Hill numbers are expressed in units of effective species and they can be extended to measure taxonomic, phylogenetic and functional diversity (Chao et al., 2014b). Local diversity patterns are influenced by environmental filtering by specific environmental variables such as temperature, precipitation, soil properties and light availability, biotic factors like species interactions including pollination and symbiosis (Cavender-Bares et al., 2009; Pavoine and Bonsall, 2011).

Turnover (beta diversity)

Beta diversity describes how species composition changes across space (Graham and Fine, 2008). Beta diversity can be partitioned in two patterns, turnover and nestedness. Turnover is the difference in species composition

between assemblages representing the replacement of species between sites, whereas nestedness occurs when assemblages with fewer species are subsets of richer assemblages, representing changes in species richness (Baselga, 2010). The differentiation of beta diversity into turnover and nestedness processes is important for addressing ecological, biogeographic and, most importantly, conservation questions that would result in different conservation strategies, given that turnover requires the preservation of a large number of sites, independently of their species richness. On the other hand, nestedness allows for the preservation of a smaller number of sites with the higher richness (Baselga, 2010; Carvalho et al., 2012). Several measures have been proposed for beta diversity however, they can be classified into two main groups, measures that analyse the variation in species richness using number of species or richness indices and measures that analyse the variation in species composition between communities using species abundances (Jurasinski et al., 2009; Koleff et al., 2003).

Regional (gamma diversity)

Gamma diversity, as alpha diversity, is used to describe the diversity present in a certain area, the difference being that gamma diversity refers to a higher spatial scale, at a regional or landscape level (Jurasinski et al., 2009). Gamma diversity is considered as "inventory diversity" and is usually calculated as the total number of species in a landscape. A common problem is that it is often derived from combining species found in individual samples, which is rarely a real representation of the species richness of the area (Jurasinski et al., 2009; Chisholm et al., 2011)

1.2 Study system

Mexican conifers

Gymnosperms are distributed in all continents except Antarctica and are of great ecological and economic importance. They consist of more than 1000 species and represent four of the five main lineages of seed plants: cycads, ginkos, gnetophytes and conifers (Wang and Ran, 2014). Conifers are the largest lineage of gymnospernms, containing 614 species in 69 genera and eight families, Pinaceae, Cupressaceae, Taxaceae, Cephalotaxaceae, Sciadopiyaceae, Podocarpaceae, Araucariaceae and Phyllocladaceae (Farjon, 2010). Conifers are a group with a varied set of ecological adaptations allowing them to occur along a wide environmental gradient (Aguirre-Gutiérrez et al., 2015). They are found in habitats from alpine tree lines to sea level (Gernandt and Pérez-De La Rosa, 2014).

Mexico is located between tropical and subtropical latitudes, Mexico is considered to be a mega diverse country with high levels of endemism (Rzedowski, 1991). It is a highly conifer-diverse country, with four families, 11 genera, 80 species and 108 infraspecific taxa, of which 61 are endemic (Farjon and Filer, 2013). Mexico harbours 43 out of the approximately 120 species of *Pinus*, seven of the 18 species of *Callitropsis*, 20 of the 68 species of *Juniperus*, eight of the 47 species of *Abies*, one out of two species of *Taxodium*, one of the four species of *Pseudotsuga* and *Calocedrus*, one of the 10 species of *Taxus*, three of the 38 species of *Picea* and 3 of the 97 species of *Podocarpus* (Farjon, 2010; Gernandt and Pérez-De La Rosa, 2014). In this thesis conifer species presence data from inventory plots of the Mexican Forestry Commission (CONAFOR) were used, where 70 native conifer species are recognised. Mexican conifers are distributed in several vegetation types, from sea level to approximately 4000 m (Gernandt and

Pérez-De La Rosa, 2014)

The genus *Pinus*, which is the largest in the Pinaceace family, is especially important due to the fact that Mexico, which is considered a secondary diversification centre of this genus along with North America, is a region of high pine species diversity (Farjon, 1996). It has been reported that Mexico harbours 43 species and 18 infraspecific taxa (Farjon, 1996); however, only 42 *Pinus* species are included in the CONAFOR data.

Historical context

Diversity patterns of conifers in the Northern Hemisphere result from multiple floristic exchanges between the Old and New Worlds (Wen et al., 2010). Conifer genera are disjunctively distributed between North America and Eurasia, with dispersal across the Bering Land Bridge and the North Atlantic Land Bridge one or more times during their evolutionary history (Wang and Ran, 2014). The genera *Abies*, *Picea*, *Pseudotsuga* and *Taxus* most likely originated in North America and migrated to the Old World. The genera *Juniperus* and *Pinus* had a Eurasian origin and migrated to North America (Wang and Ran, 2014).

The occurrence of the large diversity of pine groups in Mexico and Central America is due to the migration of pines southwards from northern North America since the mid-Cenozoic (Wang and Ran, 2014). Fossil evidence indicates *Pinus* and *Picea* presence in southern Mexico by the early Miocene and *Abies* presence since the Pliocene (Wang and Ran, 2014). This is congruent with palaeoclimate evidence that shows major temperature declines in the mid-Eocene, mid-Miocene and Neogene, suggesting the mid-Miocene as the time for the main migration of the pines to Mexico

(Richardson, 2000). Dramatic alterations in the geomorphology of Mexico, including the formation of the Sierra Madre Occidental during the Cretaceous-Cenozoic (Ferrari et al., 2005), the uplift of the Sierra Madre Oriental in the late Eocene (Eguiluz de Antuñano et al., 2000) and the formation of the Transamerican Volcanic Belt during the mid and late Miocene (Gómez-Tuena et al., 2005), together with the decrease in temperatures in the mid-Miocene and glaciations during the Pleistocene, had a great influence on the migration and diversification of pines, by opening pathways for the migration of pines from North America through both Sierra Madre Oriental and Occidental, and their subsequent adaptation to Mexico's environmental conditions through introgression and hybridisation and the development of species, subspecies, varieties and forms (Richardson, 2000). The current distribution and composition of pine forests in Mexico and Central America were probably established in the early Holocene, but were dynamic during the preceding glacial/interglacial intervals. The composition of the forests was also changing as the northern species adapted to new environments in which the temperatures decreased (Richardson, 2000).

1.3 Major questions

The main questions that are addressed in this thesis are: 1) How has the diversity of conifers in Mexico been generated and how is it currently maintained? 2) Is high gamma richness of conifers in Mexico due to high alpha or beta diversity or both? 3) Do all forms of diversity respond in the same way to environmental drivers? In order to answer these questions, conifer species data from the National Forest Inventory, conifer trait data, a phylogeny of Mexican conifers and environmental data are used.

1.4 Thesis aims

This thesis has the following aims:

1. To investigate how conifer species richness and functional diversity are influenced by environmental drivers in Mexico.

2. To explore how the distribution of conifers is shaped by environmental variables that act as environmental stressors and the phylogenetic conservatism of Mexican conifers.

3. To evaluate which beta diversity pattern, either turnover or nestedness, is dominant in Mexican conifers.

4. To analyse how the patterns of species, functional and phylogenetic beta diversity are affected and shaped by geographic distance, altitude and environmental variables.

1.5 Thesis outline

The following presents an outline of the thesis structure, together with a brief summary of how each chapter contributes to answering the main questions and to achieve the aims of this work.

- Chapter 2 gives an overview of the National Forest inventory, presents its objectives, the sampling methodology and the measured variables. Chapter 2 also explains how the inventory data were extracted, cleaned and prepared for the analysis in this thesis.

- Chapter 3 tests how conifer species richness and functional diversity are influenced by environmental drivers in Mexican forests, specifically addressing the extent to which environmental drivers act as filters

to regulate species and functional diversity in coniferous forests in Mexico.

- Chapter 4 assesses how the distribution of conifers in Mexico is driven by environmental variables that act as stressors, particularly precipitation and temperature, and the phylogenetic conservatism of conifer traits.

- Chapter 5 investigates species, functional and phylogenetic beta diversity of conifers across Mexico. It also addresses which beta diversity pattern, turnover or nestedness, is dominant in the system, and how geographic distance, altitude, or environmental variables influence beta diversity patterns.

- Chapter 6 is a synthesis of the key findings relating to the research questions and overall aims. It discusses general trends and conclusions on the maintenance and drivers of diversity patterns of Mexican conifers

Chapter 2

Forest Inventory data and pre-analysis stage

2.1 Introduction

The purpose of this chapter is to present the Forest and Soils National Inventory of the Mexican Forestry Commission (CONAFOR), its objectives, how it was designed and the data that were obtained. The process through which the inventory data were extracted and prepared for the analysis of this thesis will also be explained.

2.2 CONAFOR inventory

Background

The National Forest Inventory 2004-2009 (CONAFOR, 2009) is a follow up from the national forest inventories carried out in 1961-1985 and 1992-1994. The assessment of the forestry resources of Mexico is included in the General Law of Sustainable Forestry Development (2003), which requires that statistical and cartographic data on forest vegetation must be recorded in order to evaluate deforestation rates, their causes and to evaluate forest production values and ecosystem services. The methodology on which the inventory was based is the United Nations Food and Agriculture Organisation forest assessment.

The objectives of the National Forest Inventory were:

- To measure and obtain statistical indicators on Mexico's forest resources.
- To collect the necessary information to estimate volume, biomass and estimation of damaged trees in order to generate regional and national reports on the current status of the forest resources.
- To determine qualitative and quantitative characteristics of the forest

resources.

- To establish a methodology for the evaluation and monitoring of the forest ecosystems.
- To obtain measures of soil degradation.

Sampling methodology

Around 25,000 sampling units were established for the different vegetation types: temperate forests, tropical forests, deserts, semideserts, mangroves, among others. The sampling design and the distribution of the sampling units was based on a land use and vegetation map of Mexico made by the National Institute of Statistics and Geography (INEGI), on which a 5 km^2 grid was overlaid in order to obtain a uniform distribution of the sampling sites in all of Mexico. Sampling units for forest vegetation, based on the land use and vegetation map, were established every 5 kilometres from each other. In the National Forest Inventory, sampling units composed of four sites were used for collecting data. In the following research chapters only sampling units are considered and they will be referred to as plots or sampling sites.

Each of the four sites that compose a sampling unit are circular plots forming an inverted Y shape and separated from each other by 45.14 m to the centre of each plot. The sites measure 400 m^2. In these sites each tree with a diameter at breast height larger than 7.5 cm was measured and registered. In the 400 m^2 sites all trees were tagged and measured. All tree individuals were determined along with site geographic coordinates and site characteristics. The measured variables in the sites were classified into quantitative and qualitative variables (Table 2.1)

Table 2.1: Measured variables in each of the sites.

Quantitative variables	Qualitative variables
Tree number	Species
Height	Common name
Diameter at breast height	Taxonomic group
Crown diameter	Species conservation status
Vegetation cover	Vegetation type
Altitude	Disturbance type
Slope	Tree damage
Facing	Condition (dead or alive)
Soil depth	

2.3 Data Cleaning

Firstly, the geographic coordinates and altitude of each sampling unit were obtained by filtering the sampling site located in the middle of each sampling unit (site 1) with its corresponding coordinates. Sampling units without geographic coordinates assigned to them were not considered in the analysis. In order to retrieve the relevant tree data for the analysis, as the taxonomic family to which the species belong is listed in the inventory database, the conifer families that are native to Mexico according to Farjon (2010) were filtered, along with their respective genera, species and sampling unit. A list of the inventory's conifer species and a list of the conifer species that are considered native to Mexico according to Farjon (2010) were cross referenced and non-native species were left out of the data set. Records with an incomplete taxonomic classification were not considered in further analysis. The data were extracted, cleaned and prepared to be analysed using R programming language (R Core Team, 2019).

The inventory sampling units for forest vegetation was composed of 10,895

records. After filtering only the sampling units with presence of conifers native to Mexico, the database was left with 6,963 sampling units (Figure 2.1). Sampling units with absence of conifer species were excluded from the analyses. In terms of conifer individuals, the inventory data for forest vegetation had 757,614 records. However, after filtering only gymnosperm species and discarding non native species to Mexico, the database was left with 198,013 records and a total of 70 conifer species. The full list of conifer species recognised by the National Forest Inventory and the number of individuals of each species are included as supplementary material (Appendix A: Table A.1).

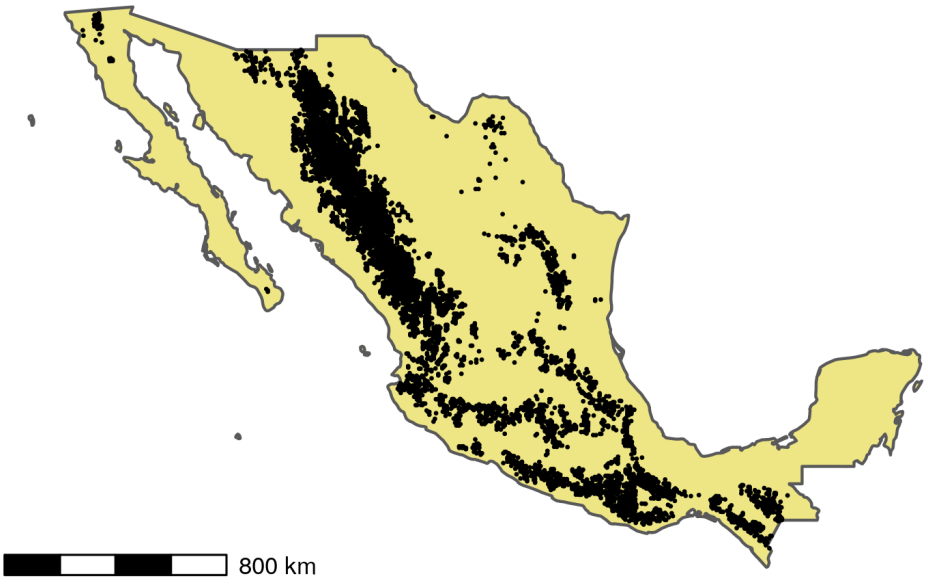


Figure 2.1: Distribution of the National Forest Inventory sampling units with presence of conifers in Mexico

Chapter 3

Trait based tree coexistence mechanisms in Mexican coniferous forests

3.1 Introduction

Trait-based ecology is a valuable tool for the study of community assembly and species coexistence (Chacón-Labella et al., 2016; Escudero and Valladares, 2016). Traits are measurable and defined properties of an organism that can be used across species, scales and environments (Shipley et al., 2016). Compared to the nomenclatural approach, based on taxonomy and species identities (McGill et al., 2006; Shipley et al., 2016), a trait-based perspective offers a more generalised and mechanistic comprehension of the ecological processes that shape community assembly (Chacón-Labella et al., 2016).

The relationship between species traits and the environment in which they occur has been an important topic in community ecology, where the objective is usually to be able to predict which traits, and hence species, are linked to a certain set of environmental conditions (Keddy, 1992). For a species to be part of a community it requires the appropriate traits to establish in the site, as plant traits affect the performance of individuals (Lebrija-Trejos et al., 2010). One of the proposed determinants in shaping species composition is environmental filtering, which occurs when a species lacks the ability to tolerate local environmental conditions, preventing it from establishing (Šímová et al., 2015). The co-occurrence of ecologically similar species is thought to be caused by environmental filtering (Keddy, 1992).

Mean and variance of trait values have been used to explore the effect of environmental filtering on assemblage composition (Šímová et al., 2015). Mean trait values indicate overall species composition, while variance of trait values indicates the size of the occupied niche space (Šímová et al., 2015). It is assumed that environmental stressors, such as temperature and precipitation extremes, result in stronger environmental filtering, and a re-

duction in trait variance (Kluge and Kessler, 2011; Šímová et al., 2015). Despite this assumption, Coyle et al. (2014) found that for eastern North American tree communities, trait diversity was weakly responsive to environmental filtering caused by stress gradients of water and soil nutrient availability. A negative relationship was found between seed mass diversity and water deficit, defined as the difference between potential evapotranspiration and actual evapotranspiration over the course of one year. Also trait diversity reached a minimum for wood density towards the middle of the soil nutrient availability gradient. Similarly in North America, Šímová et al. (2015) found that trait variance did not significantly decrease with stressful climatic conditions, in this case temperature and precipitation. Nonetheless, they found shifts in the mean trait values, indicating trait filtering induced by climate. In South American seasonal tropical forests, where precipitation seasonality was positively correlated with high levels of trait diversity in angiosperms, this relationship seems to be caused by the co-occurrence of functional strategies (Swenson et al., 2012). In North American temperate forests, functional diversity is reduced with temperature seasonality but not precipitation seasonality (Swenson et al., 2012). Species richness has been reported to increase with precipitation and temperature, and to decrease in wetter and cold or warm and dry climates (Currie, 1991). The combination of high temperature and precipitation generally results in more suitable conditions for plants, and has been a strong predictor for greater height, wood density, specific leaf area and seed mass in North American trees (Šímová et al., 2015). At local scale, woody plant species richness in the Mediterranean region of Chile is driven by precipitation and temperature (Becerra, 2016).

Mexico is a highly conifer-diverse country, with four of the eight extant families, 11 genera, 80 species and 108 infraspecific taxa of which 61 are

endemic (Farjon and Filer, 2013). Conifers are a group with a varied set of ecological adaptations allowing them to occur along a wide environmental gradient (Aguirre-Gutiérrez et al., 2015). They are found in habitats from alpine tree lines to sea level (Gernandt and Pérez-De La Rosa, 2014).

This chapter aimed to test how coniferous species richness and functional diversity are influenced by climatic drivers. I expected species richness would decrease with stressful and seasonal climates particularly: a) that species richness would peak around the midpoint of mean annual temperature, annual precipitation, precipitation of the warmest quarter, altitude and soil depth. b) Species richness would decrease in response to temperature and precipitation seasonality. c) An increase in species richness and functional diversity would occur with the interaction of precipitation and temperature. d) Functional richness and functional dispersion would be constrained under stressful conditions.

This study sought to describe and interpret macroecological patterns of conifer diversity across Mexico, incorporating species richness and functional traits. I tested the extent to which environmental drivers act as filters to regulate functional diversity in forest assemblages in Mexico at biogeographical scales.

3.2 Methods

Forest inventory data

Species occurrences were obtained from the Forest and Soils National Inventory of the Mexican Forestry Commission (CONAFOR, 2009) . The National Forest Inventory protocol records trees $\geq$ 7.5 cm diameter at breast height in four 400 m^2 sites, which together form a sampling unit used in this study. Angiosperm records and conifer species not native to Mexico according to Farjon (2010) were excluded. Incomplete records in terms of species name and location, or with geographical coordinates corresponding to locations outside Mexico were also excluded. After data cleaning, 6963 site records were left to be used in the analysis. A total of 198,013 individuals belonging to 70 species representing eight genera and four families, according to APG III (Bremer et al., 2009), were included in the analysis.

Species trait data

A trait matrix was constructed using seven traits of Mexican conifer species extracted from literature descriptions from Farjon (2010) and online databases (Table 3.1). Leaf area was calculated by multiplying the length and width of the leaves, whereas the cone size was measured as the length/width ratio of the cones. Trait data on some of the conifers species was not available, this was the case for wood density on 11 species, bark thickness on four species and seed size data on three species. Trait records absences were included in the analysis as NAs. Functional diversity indices were computed using the R package FD (Laliberté et al., 2014), which allows for missing trait values. The functional diversity indices functional richness (FRic) and functional dispersion (FDis) were calculated in each sampling site using a multi trait approach (Lefcheck et al., 2015). FRic represents the amount of

functional space filled by a given assemblage (Villéger 2008) and is used to estimate the dispersion of species in the trait space, while FDis measures the dispersion of the individual species in trait space as the mean distance to the centroid of all species in the assemblage or grid cell (Laliberte et al., 2010).

Table 3.1: Traits used in the analysis: minimum, maximum and mean values across species.

Trait	Min.	Max.	Mean	Source
Height (m)	5	100	28.67	Farjon, 2010
Seed size (g)	3.82	1260	119.05	Kew Millennium Seed Bank Project
Bark thickness (cm)	0.55	8.10	4.34	Farjon, 2010
Diameter at breast height (cm)	20	550	108.85	Farjon, 2010
Wood density (mg/cm^3)	0.33	0.61	0.44	Zanne et al., 2009
Leaf area (cm)	0.02	19.95	3.06	Farjon, 2010
Cone size (cm)	0.1	3.7	1.48	Farjon, 2010

Environmental data

Eight environmental variables (Table 3.2) were selected to examine the relationship between the environment and species richness and the indices of functional diversity. Five variables, annual mean precipitation, temperature seasonality, annual precipitation, precipitation seasonality and precipitation of the warmest month were extracted at 30 arcsec resolution (Cuervo-Robayo et al., 2014). Mean values of these variables were calculated for each site using the extract function from the raster R package. Altitude, soil depth, and slope aspect were obtained from the Forest and Soils National Inventory of the Mexican Forestry Commission (CONAFOR, 2009) at site level. Stressful climate was defined as low precipitation, low temperature, or high seasonality within the range observed in Mexico.

Table 3.2: Environmental variables used in the analysis, minimum, maximum and mean values and sources.

Environmental variables	Min.	Max.	Mean	Source
Annual mean temperature (°C)	5.70	26.67	14.76	Cuervo-Robayo et al., 2014
Temperature seasonality (%)	0.15	2.43	1.15	Cuervo-Robayo et al., 2014
Annual precipitation (mm)	139.49	3073.48	882.71	Cuervo-Robayo et al., 2014
Precipitation seasonality (%)	48.97	146.58	95.40	Cuervo-Robayo et al., 2014
Precipitation of the warmest quarter (mm)	11.87	955.51	375.62	Cuervo-Robayo et al., 2014
Altitude (m)	0.11	3900	2091.2	CONAFOR, 2009
Soil depth (cm)	0	265	30.55	CONAFOR, 2009
Slope aspect				CONAFOR, 2009

Slope aspect is a categorical variable, minimum, maximum and mean values were not calculated.

Statistical analysis

Patterns of species richness and functional diversity

The relationships between species richness and the indices of functional diversity and the environmental predictors were described using generalised linear models (GLMs). Polynomial terms of annual mean temperature, annual precipitation, precipitation of the warmest quarter, altitude and soil depth were included to detect nonlinear patterns. An interaction term between annual mean temperature and annual precipitation was included in the models. Functional dispersion was analysed as a zero-inflated model, which is a two-step process, a GLM binary analysis with a binomial logistic regression for the binary fraction of the data and a GLM continuous analysis for the non-zero fraction of the data (Zuur et al., 2009). For species richness two different error distributions were postulated for the models, Gaussian and Poisson. Akaike information criterion (AICc) values were used to select the best model (Burnham and Anderson, 2002). A Gaussian distribution was selected for functional richness and the presence-only fraction of func-

tional dispersion. A binomial error distribution was used for the binary fraction of functional dispersion. All analyses were performed using R programming language (R Core Team, 2019).

3.3 Results

Environmental influence on species abundance and functional diversity

Species richness increased with temperature seasonality, precipitation of the warmest quarter, altitude, and the interaction between annual mean temperature and annual precipitation, and decreased with annual mean temperature, annual precipitation, and flat slope (Table 3.3, Fig. 3.1). Functional richness increased in response to temperature seasonality, annual precipitation, altitude, the interaction between annual mean temperature, and northeast and west-facing slopes, and decreased with annual mean temperature, precipitation seasonality, and south and flat slope (Table 3.3, Fig. 3.2). Functional richness peaked at around 1000mm of annual precipitation before declining, producing a hump-shaped relationship (Fig. 3.2c). Precipitation of the warmest quarter presents a similar pattern for both species and functional richness, in which they peaked around 500 mm of precipitation (Fig. 3.1e, Fig. 3.2e).

In the case of functional dispersion, the binary fraction of the zero-inflated model shows a significant positive effect of temperature seasonality, annual precipitation, precipitation of the warmest quarter, the interaction between annual mean temperature and annual precipitation, altitude and soil depth, and a negative effect of annual mean temperature and southeast-facing slope (Table 3.3, Fig. 3.3). For the non-zero fraction, there is a significant positive effect of precipitation of the warmest quarter, and the interaction between annual mean temperature and annual precipitation, and a negative effect of annual mean temperature, annual precipitation, and precipitation seasonality (Table 3.3, Fig. 3.4).

Table 3.3: Generalised linear models describing variation in species abundance, functional richness, and functional dispersion. The best model according to AIC is reported. Blank cells indicate variables not included in the best model for that metric.

	Species richness		Functional richness		Functional dispersion			
					Binary fraction		Non-zero fraction	
	Estimate	Pr(>|t|)	Estimate	Pr(>|t|)	Estimate	Pr(>|t|)	Estimate	Pr(>|t|)
Intercept	1.494	0.238	0.080	0.028	1.178	0.162	0.134	<0.001
Annual mean temperature	**-0.179**	<0.001	**-0.015**	<0.001	**-0.431**	<0.001	**-9.77x10^{-3}**	<0.001
Annual mean temperature^2	**1.40x10^{-3}**	0.042	**2.36x10^{-4}**	0.026	9.88x10^{-4}	0.708	**2.09x10^{-4}**	<0.001
Temperature seasonality	**0.344**	<0.001	**0.018**	<0.001	**1.272**	<0.001	2.85x10^{-3}	0.115
Annual precipitation	2.57x10^{-4}	0.154	**1.16x10^{-4}**	<0.001	**1.24x10^{-3}**	0.044	1.10x10^{-5}	0.366
Annual precipitation^2	**-7.70x10^{-7}**	<0.001	**-9.25x10^{-8}**	<0.001	**-2.41x10^{-6}**	<0.001	**-2.54x10^{-8}**	<0.001
Precipitation seasonality	-1.25x10^{-3}	0.116	**-3.95x10^{-4}**	<0.001	-2.35x10^{-3}	0.344	**-2.24x10^{-4}**	<0.001
Precipitation of the warmest quarter^2	**7.70x10^{-7}**	<0.001	3.67x10^{-9}	0.846	**2.09x10^{-6}**	<0.001	**1.54x10^{-8}**	0.025

Annual mean temperature:	**$8.99\text{x}10^{-5}$**	<0.001	**$6.05\text{x}10^{-6}$**	<0.001	**$2.50\text{x}10^{-4}$**	<0.001	**$2.72\text{x}10^{-6}$**	<0.001
Annual precipitation	**$7.12\text{x}10^{-8}$**	<0.001	**$6.63\text{x}10^{-9}$**	<0.001	**$2.78\text{x}10^{-7}$**	<0.001	$6.97\text{x}10^{10}$	0.080
Altitude^2	$6.61\text{x}10^{-6}$	0.068	$-3.55\text{x}10^{-7}$	0.290	**$4.92\text{x}10^{-5}$**	<0.001		
Soil depth^2	0.020	0.515	**$7.60\text{x}10^{-3}$**	0.014	-0.050	0.653		
Northeast aspect	$-8.38\text{x}10^{-4}$	0.981	$6.34\text{x}10^{-3}$	0.073	$-9.53\text{x}10^{-3}$	0.940		
Northwest aspect	$-4.62\text{x}10^{-3}$	0.894	$5.51\text{x}10^{-3}$	0.113	-0.028	0.816		
North aspect	0.045	0.203	**$6.88\text{x}10^{-3}$**	0.048	0.051	0.688		
West aspect	-0.046	0.202	**$-7.54\text{x}10^{-3}$**	0.033	-0.151	0.234		
South aspect	-0.065	0.068	$2.80\text{x}10^{-3}$	0.436	**-0.266**	0.032		
Southeast aspect	$2.59\text{x}10^{-}3$	0.942	$2.84\text{x}10^{-3}$	0.419	$-6.04\text{x}10^{-3}$	0.962		
Southwest aspect	**-0.097**	0.018	**$-9.90\text{x}10^{-3}$**	0.012	-0.200	0.173		
Flat aspect								

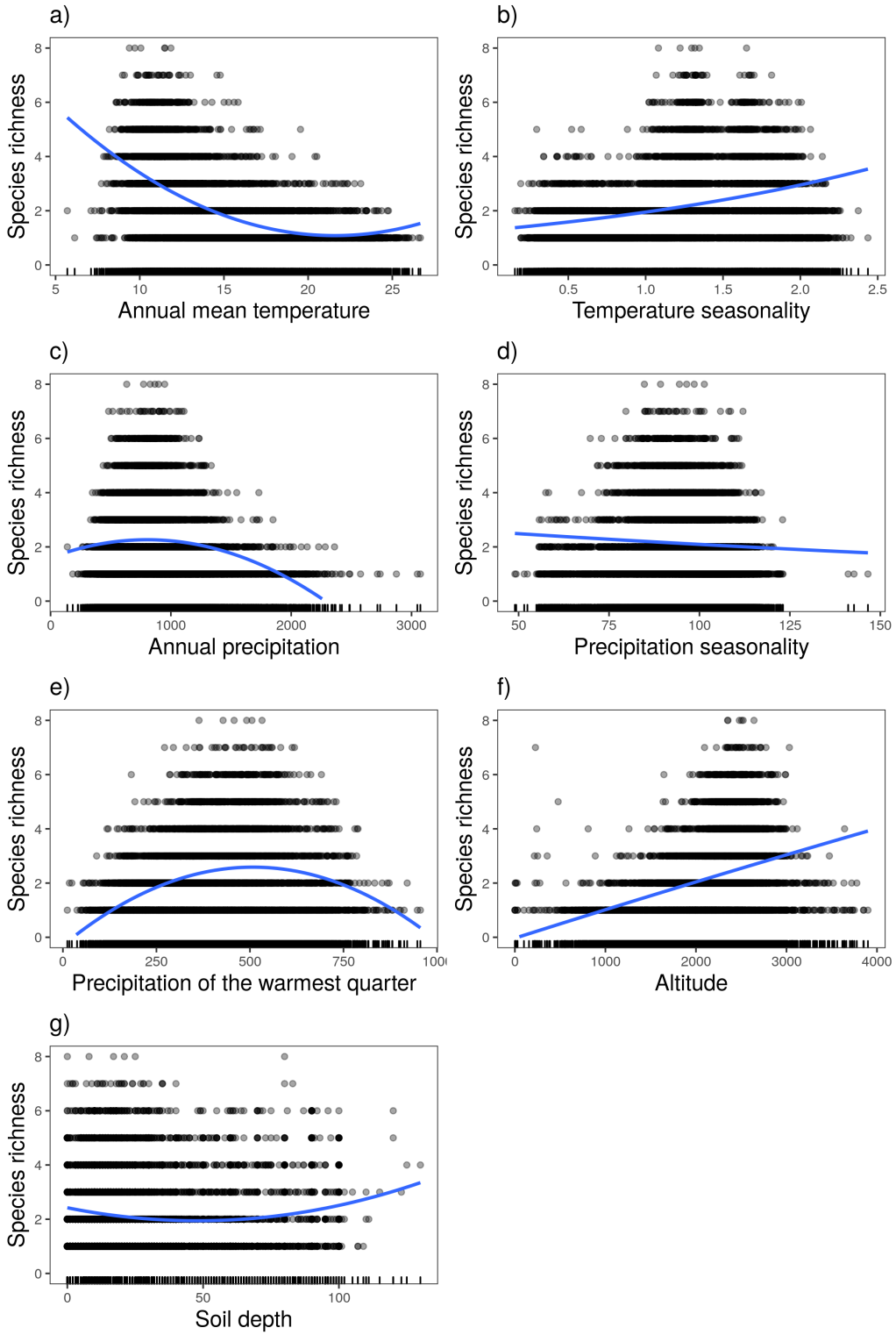


Figure 3.1: Correlation between species richness and the environmental variables. Lines are a spline fit.

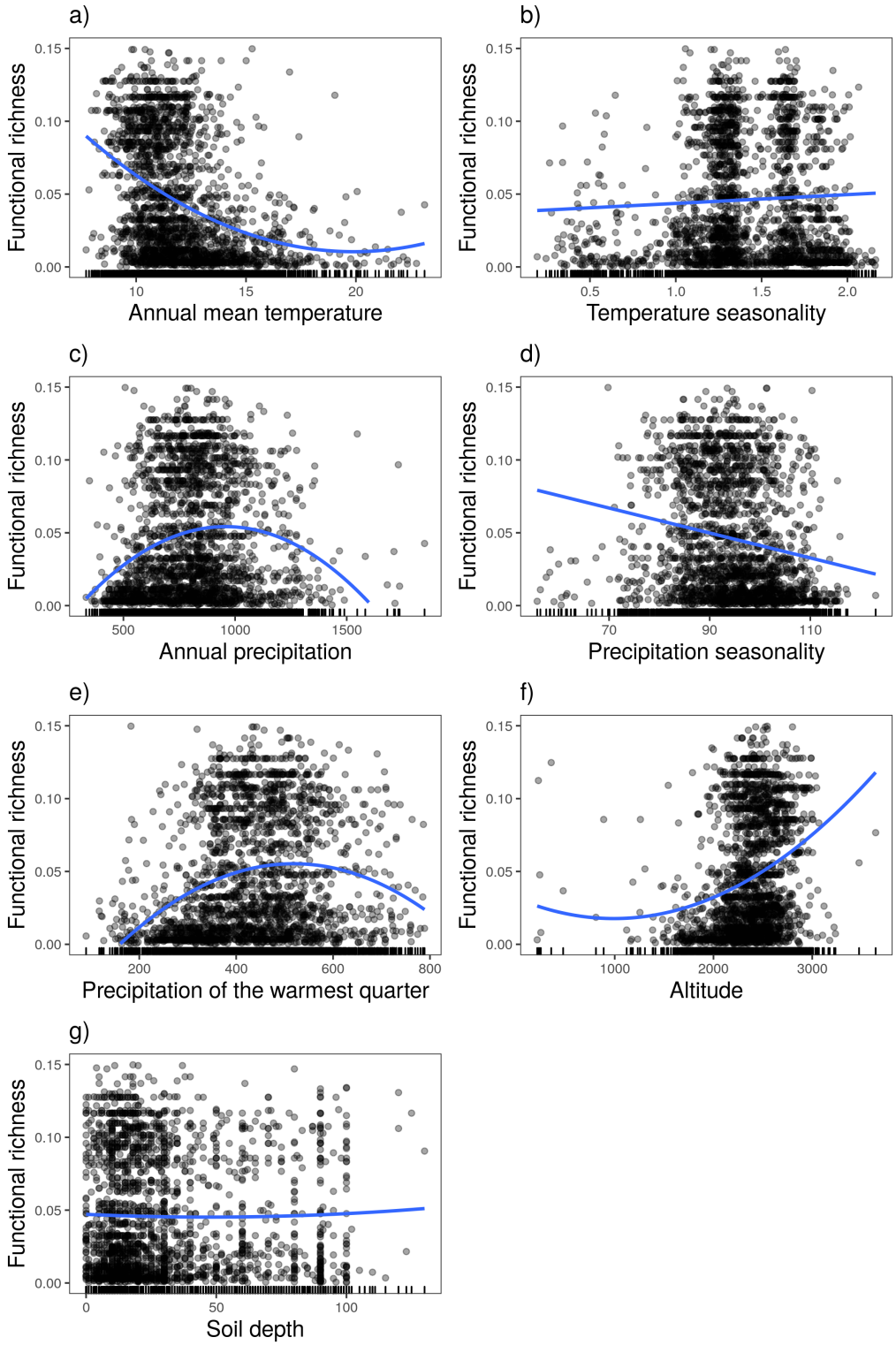


Figure 3.2: Correlation between functional richness and the environmental variables. Lines are a spline fit.

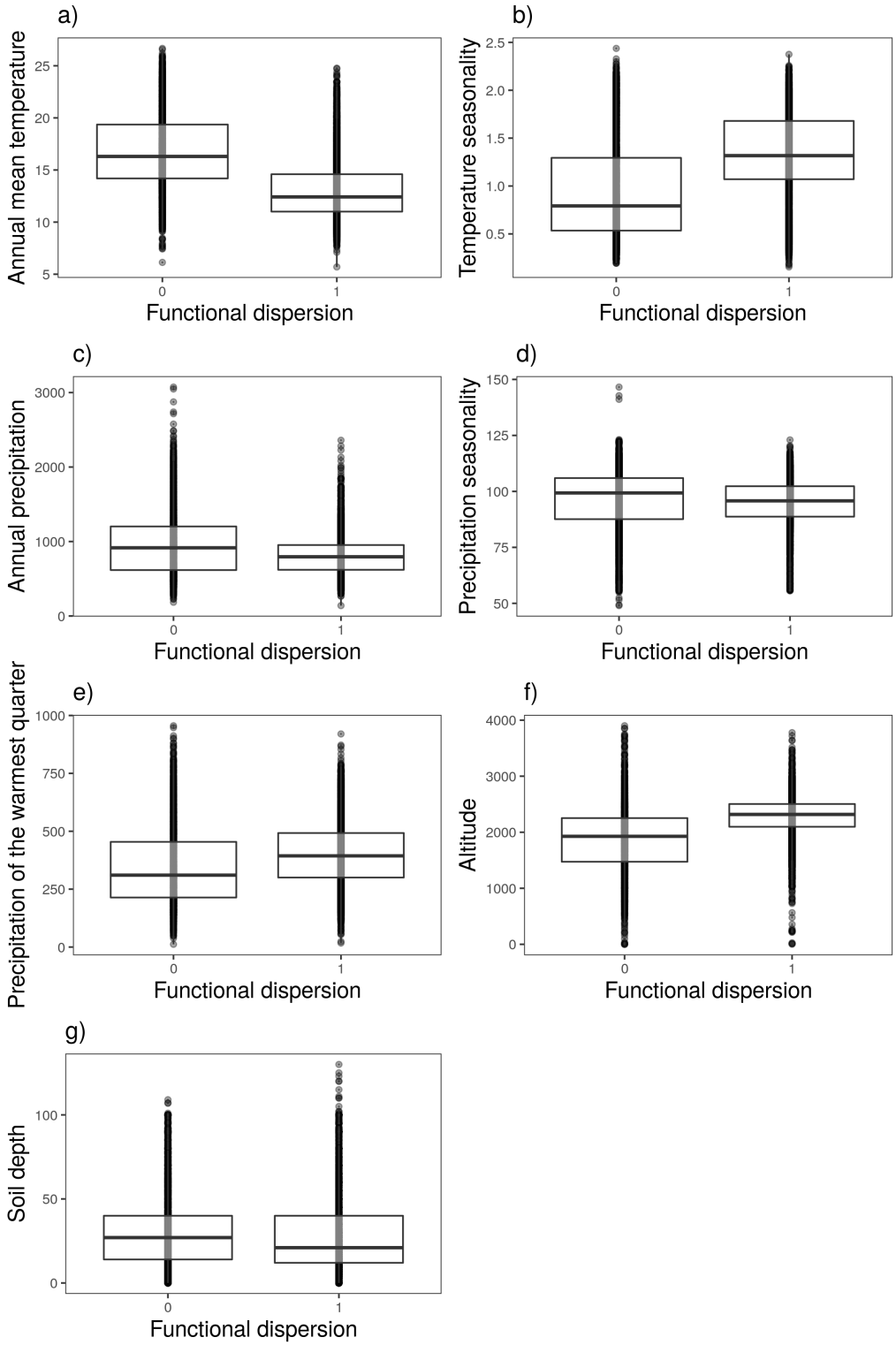


Figure 3.3: Boxplots of the environmental variables and the binary fraction of functional dispersion.

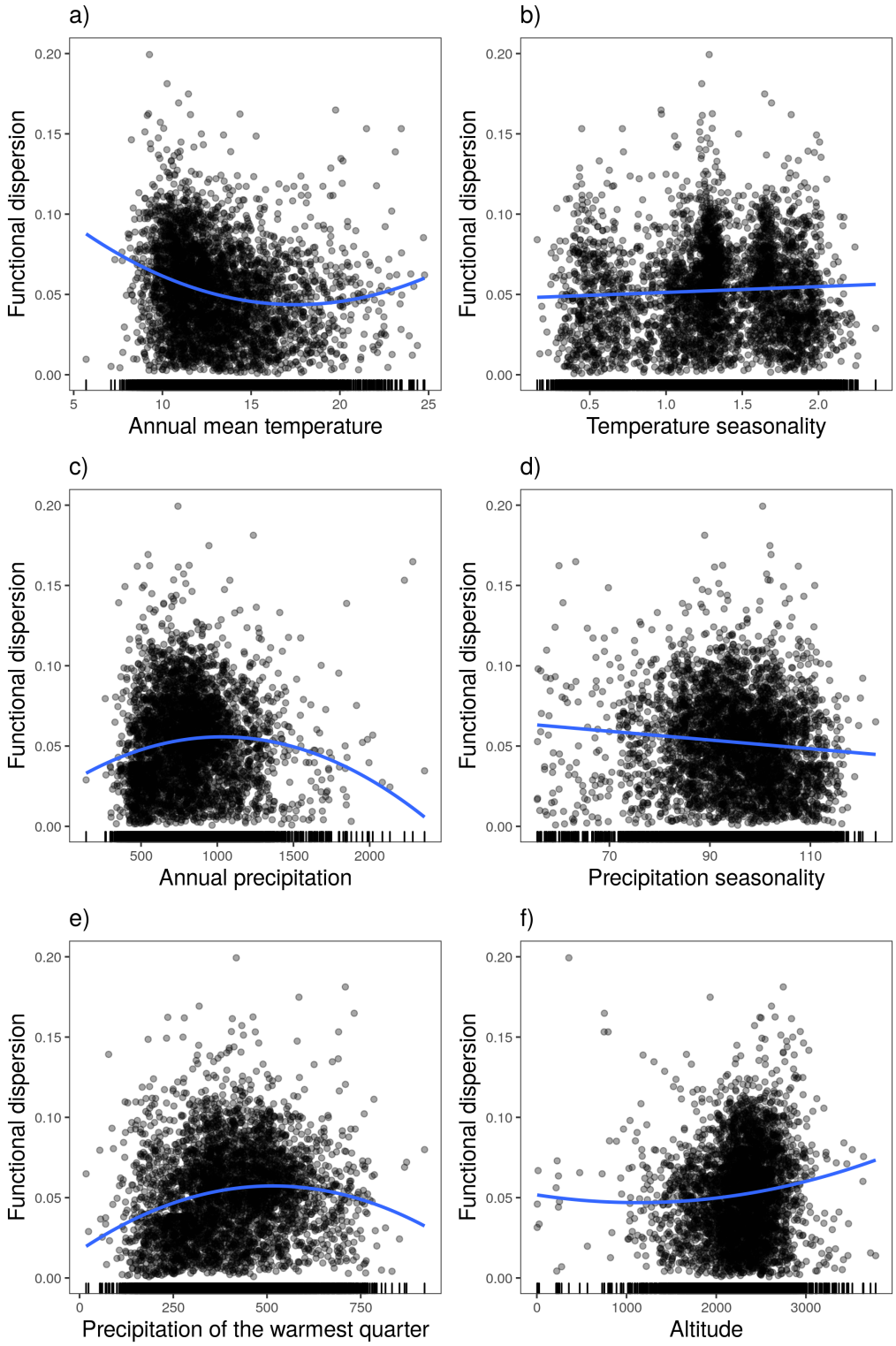


Figure 3.4: Correlation between the non-zero fraction of functional dispersion and the environmental variables. Lines are a spline fit.

3.4 Discussion

The aim of this chapter was to provide insight to the species richness, functional diversity and environmental drivers that are present in Mexican coniferous forests by using georeferenced occurrence data of conifer species, a species trait database and environmental variables.

I found that annual mean temperature has a negative effect on species richness, contrary to its effect on tree richness in the boreal forest of southwest Yukon in Canada (Paudel et al., 2016), but consistent with a larger scale study that covered the entire range of Canada's forested ecosystems, where species richness declines with temperature (Zhang et al., 2014b). The direction of the effect of mean annual temperature and precipitation on species richness might be dependent on the spatial scale, from a temperate regional scale to a national scale in China, where Zhang et al. (2017) found that mean annual temperature has a negative effect on plant species richness in the temperate nature reserves of Shandong Province, and a positive effect at a national scale, whereas mean annual precipitation has a positive effect on temperate plant species richness at both province and national scale. Precipitation of the warmest quarter showed a positive effect on species richness. This was consistent with Qian el al. (2016), who found a strong correlation of precipitation of the warmest quarter and species richness of angiosperm trees in China.

Altitude had a positive effect on species richness, consistent with Xu el al. (2016), where the elevational range was the most important factor for vascular plant species richness in China at a national scale. Their study also found that at a smaller, regional level, elevational range was positively related to plant richness when it was less than 1,900 m, but non-significant when the elevational range was larger than 1,900 m. They attribute this to

the low availability of energy at higher elevations, mainly annual potential evapotranspiration.

Soil depth does not influence conifer species richness, although in Canada's boreal forest, edaphic variables have a strong influence on tree richness where variables such as woody debris, texture, organic layer depth, and rooting zone depth were taken into account (Paudel et al., 2016). Johnstone el al. (2010) suggests that the decline of deciduous species in conifer-dominated sites of boreal forests in Alaska is caused by the effect of coniferous trees on soil characteristics. I did not have access to data on these variables.

I expected temperature and precipitation seasonality to have a negative effect on species richness. In fact, temperature seasonality has a significant positive effect on species richness. Similar results were reported for woody plant species from China at a provincial scale (Qian, 2013), and for plant species richness in a Borneo-wide scale (Raes et al., 2009). Precipitation seasonality did not have a significant effect on conifer species richness in Mexico. For vascular species richness in China, Xu el al. (2016) found that precipitation seasonality is an important environmental variable at a national scale and in the Eastern Monsoon and the Qinghai-Tibetan Plateau regions. I also found that the interaction term of annual mean temperature and annual precipitation had a positive effect on species richness.

A multi-trait approach was used to quantify functional diversity indices in order to obtain a complete characterisation of the functional diversity of the species (Lefcheck et al., 2015). Functional trait diversity is expected to be constrained under harsh environmental conditions (Swenson et al., 2012; Weiher and Keddy, 1995). Annual mean temperature showed a neg-

ative effect on functional richness and functional dispersion, while annual precipitation had a positive effect on both indices of functional diversity. Schellenberger Costa et al. (2017) found that temperature and precipitation had a negative effect on plant's functional dispersion on Mount Kilimanjaro. I found that the interaction term of annual mean temperature and annual precipitation had a positive effect on functional richness and functional dispersion. Similarly, Šímová et al. (2015) found that the interaction of temperature and precipitation was the best predictor for trait diversity

Precipitation seasonality was found to have a negative effect on functional richness and functional dispersion. Conversely to Swenson et al. (2012) who found that precipitation seasonality was positively correlated with functional diversity in seasonal forests of Brazil and Central America. However they hypothesised that functional diversity in seasonal forests is higher because of their high number of species, and because of the pressure of precipitation seasonality which causes a great variety of functional strategies to co-occur in that region. I found temperature seasonality to have a positive effect on functional richness and functional dispersion, contrary to Swenson el al. (2012) who found temperature seasonality to have a negative effect on functional diversity in temperate regions of North America.

Soil depth did not have a significant effect on functional richness. However it did showed a significant positive effect on functional dispersion. Schneider et al. (2017) reported that, in a mountain temperate mixed forest in Switzerland, functional richness was constrained towards the mountain ridge, which presents stressful conditions such as dry, shallow and rocky soil, high elevation, steep slopes, and high solar radiation. These conditions act as environmental filters allowing species with certain functional traits to exist in that area (Schneider et al., 2017). Altitude had positive

effect on functional richness and functional dispersion. In a broad-leaved forest in China, altitude and soil depth have a positive correlation with functional dispersion (Zhang et al., 2017a). In the Appalachian forests of eastern North America, functional richness was higher in areas with low soil fertility at high and low elevations where coniferous species co-occur with broad-leaved species, increasing the functional richness values (Chapman and Mcewan, 2018).

The results of this chapter showed that species richness and functional diversity are influenced by climatic drivers to varying extents. Annual mean temperature and annual precipitation both had a negative effect on species richness. For functional diversity, annual mean temperature and annual temperature had opposite effects: a negative effect from temperature and a positive one from precipitation. An unexpected result was that temperature seasonality had a positive effect on species richness and functional diversity, and precipitation seasonality only had a negative effect on functional richness. This is consistent with the findings regarding seasonal climate in temperate zones in North America (Swenson et al., 2012) suggests that stressful climate does not necessarily limit functional diversity. The effect of altitude was overall positive for species richness and functional diversity, peaking in mid to high altitudes. The positive effect of the interaction of temperature and precipitation in species richness and both functional richness and dispersion shows that, in this study system, the combination of high temperature and precipitation result in conditions that are more suitable for plants.

Living conifers are a successful group with broad distribution in woody plant biomes, with the exception of lowland equatorial rain forests where conditions such as high productivity and light competition make it a hostile

environment for needle-leaved conifers (Brodribb and Hill, 1997), as is the case of the Yucatan Peninsula in the south of Mexico. While the reason why particularly Pinaceae species have not been able to disperse into the Southern Hemisphere alpine and temperate zones is still unresolved, there is evidence of a rapid increase of angiosperms in the equatorial zone during the Cenozoic which created a highly productive and shaded rain forest belt hostile to Pinaceae (Boyce et al., 2010). Several hypotheses have been formulated for trying to explain the proliferation of angiosperms after the Cretaceous, for example hypothesis about plant carbon economy, resistance to climatic stress, nutrient economy, biotic interactions and diversification (Augusto et al., 2014). The carbon economy hypothesis proposes that angiosperms dominated gymnosperms through an increased growth rate; however, this hypothesis might only be viable in tropical climates with productive and rich soils and not in harsh environments where angiosperms also thrive. The climate hypothesis proposes that dry conditions at the end of the Eocene caused the extinction of ancient gymnosperms that were not able to tolerate such conditions, and that angiosperms could not fully establish themselves in cold environments because conifers outperform angiosperms in frost tolerance. The nutrient economy hypothesis states the gymnosperms are have an adaptation to low-nutrients soils and because of that, an increase in nutrient availability will be a driver of angiosperms dominance. The biotic interaction hypothesis suggests that morphological innovations acted as advantages particularly as pollination and seed dispersal strategies, on the other hand, the diversification hypothesis proposes that a rapid diversification of angiosperms originated new lineages with high diversity of forms and functions with potential to occupy diverse niches (Augusto et al., 2014). It appears more feasible that a multiple hypothesis approach can better explain the rise and dominance of angiosperms in certain regions, with plant carbon economy and diversification responsible for the early rise

of angiosperms and tolerance to climatic stress, nutrient economy, biotic interactions and late angiosperm diversification responsible for the expansion and establishment of angiosperms (Augusto et al., 2014).

As mentioned in section 2.3, sampling units with absence of conifers, hence with angiosperm species presence only, were deliberately excluded from the analyses. The decision to completely exclude angiosperms from the analysis probably had an impact in the results, as species absent from community samples provide valuable information for understanding community patterns and their underlying processes (Pärtel, 2014). Similar to forests in Mexico, forest systems at higher latitudes and altitudes harbour a mixture of conifers and angiosperms (Brodribb and Hill, 1997). Angiosperms are an important component of many Mexican tree communities. In order to fully understand the drivers of conifer diversity in Mexico, angiosperm presence and communities where angiosperms are dominant in the absence of gymnosperms must be considered. Such dataset would include a large proportion of sites with absences of conifers represented as zero values. When a dataset contains a large proportion of zero values is referred to as zero inflated, moreover, zero values can be classified into two types of zero, true zeros and false zeros. True zeros occur as a result of a low frequency occurrence of the species either because of its life history or unsuitable habitat, they can also occur by chance because the species does not saturate its habitat due to local extinctions, on the other hand, false zeros are caused by failing to record a species that inhabits a site even if it inhabits the site either because it was not present at the time of the survey, inadequate sampling method or because the observer was unable to detect it (Martin et al., 2005). The approach to analyse a zero inflated dataset will depend on the type of zero. In the case of true zeros, zero-inflated models such as two-part models and mixture models are recommended, two-part modelling consist

first on a binary outcome model and then on a truncated count model, it assumes that the zeros arise from a single process; mixture models are composed of probability distributions that represent two or more ecological processes, usually with a zero-inflated Poisson model. For false zeros, zero-inflated mixture modelling is suggested as two ecological processes, one leading to true zeros and another one to false zeros would require modelling (Martin et al., 2005). A possible approach for a scenario where the Mexican conifers dataset were to include sites with absences of conifers represented as zero values and regarded as zero-inflated, would be to treat the zeros as true zeros, this because conifer absence is most likely due to habitat unsuitability, and to use a zero-inflated Poisson model.

Chapter 4

Environmental trait associations and trait evolution in Mexican coniferous forests

4.1 Introduction

Understanding the ecological and evolutionary processes that shape and drive biodiversity patterns has been a long time challenge for the study of biodiversity (Pavoine and Bonsall, 2011; Šímová et al., 2015). Biodiversity is usually explored through species diversity metrics, particularly species richness. On the contrary other components of diversity have been less considered, even though biodiversity is regarded as a complex concept that includes taxonomy, traits and phylogenetic aspects of species (Pavoine and Bonsall, 2011). Functional and phylogenetic diversity have been increasingly used to provide insights into the drivers of biodiversity patterns (Swenson, 2013).

Species traits and their function are considered to have an important role in the distribution of species, particularly when considering the association of the assemblages functional diversity and the abiotic filtering along environmental gradients (Swenson et al., 2012). Environmental filtering occurs when a species is unable to establish in a location given that it lacks the necessary attributes in order to tolerate the local environment (Šímová et al., 2015). Environmental filtering is expected to constrain functional diversity, with the strongest filtering occurring in the locations with the least favourable conditions along an environmental gradient (Swenson et al., 2012).

Environmental stressors such as seasonality and extreme temperature and precipitation are expected to increase environmental filtering (Kluge and Kessler, 2011). The ability to tolerate environmental stress has a strong influence on species distributions (Rueda et al., 2017). In general plant distributions are driven to a great extent by temperature extremes and by water and light availability (Kunstler et al., 2016). Gymnosperms, in

particular conifers, are more drought resistant as a result of several strategies, for example they have a lower stromatal sensitivity to vapour pressure deficit and a cavitation-resistant xylem made up entirely of tracheids (Moran et al., 2017). Several conifer species are a dominant component of many arid forests environments (Moran et al., 2017).

Conifer distribution appears to be influenced by geographic characteristics at continental scales. In the Northern Hemisphere recently diverged conifer species are mainly concentrated in mountainous areas of North America and southern China (Leslie et al., 2012). These patters are attributed to the range of environments present in the area together with the history of trait evolution in conifers (Rueda et al., 2017). Functional traits of present day conifers represent an evolutionary response to environmental stressors that have an influence on species on a range of geographic scales and across evolutionary time; therefore, distinguishing the distributions of conifer traits and their underlying environmental stressors has implications for understanding the presence of conifers in certain areas (Rueda et al., 2017).

Gymnosperms, including conifers, had a widespread distribution during the Permian period, which became warm and arid towards its end (Crisp and Cook, 2011). Even though most Permian conifer ancestors are extinct and living conifers are the result of post-Eocene radiations, present day conifer species are the result of retained ancestral characters and their evolutionary responses to the environmental changes that have occurred during the last 34 million years of the Cenozoic (Rueda et al., 2017). Conifer species distributed in Mexico have an affinity to arid environments, in particular species of the genus *Pinus* and *Juniperus* in the regions of the Sierra Madre Oriental, Sierra Madre Occidental and the Transverse Volcanic Belt in the

north east, north west and across central Mexico respectively (Farjon, 1996; Mao et al., 2010).

The tendency of lineages to retain their niche-related traits through speciation events and over macroevolutionary time, including the traits related to a response to environmental stressors, is called phylogenetic niche conservatism (Crisp and Cook, 2012). A strong pattern of phylogenetic niche conservatism among extant species could reflect the retention of niche-related traits of their ancestors during their diversification (Prinzing et al., 2001). Phylogenetic niche conservatism has a strong influence in community composition, by the filtering of the regional species pool based on environmental niche parameters (Donoghue, 2008).

In this chapter I use functional trait conifer data, a conifer phylogeny and environmental data to investigate how the distribution of conifers is influenced by environmental variables that act as environmental stressors and lead to phylogenetic conservatism in Mexican conifers. Two main predictions are addressed: that (a) drought-related trait distributions would be explained by aridity-related environmental variables, (b) presence of phylogenetic niche conservatism would occur in traits related to environmental stressors, particularly the ones related to aridity and temperature.

I address this predictions by (a) mapping the distributions of conifer traits in Mexico in order to assess their geographical patterns, (b) testing the relationships between the geographic distributions of each trait and the environmental variables, (c) determining the presence of phylogenetic niche conservatism for each trait, d) testing correlations between environment and species traits while accounting for their phylogeny.

4.2 Methods

Study area

The study area is comprised of the complete native distribution of Mexican coniferous forests (Fig. 4.1). As a result of a complex climatic and geological history, combined with anthropogenic impacts, the coniferous forest is patchily distributed along the mountain ranges of Mexico. There are two important north-south mountain ranges: the Sierra Madre Occidental in the west, reaching heights of 3,000 m, and the Sierra Madre Oriental in the east, reaching almost 4,000 m. In the Northwest, the Sierra de Baja California extends from Southern California down the Baja California Peninsula into Baja California Sur state, reaching an altitude of 1980 m (Perry, 1991).

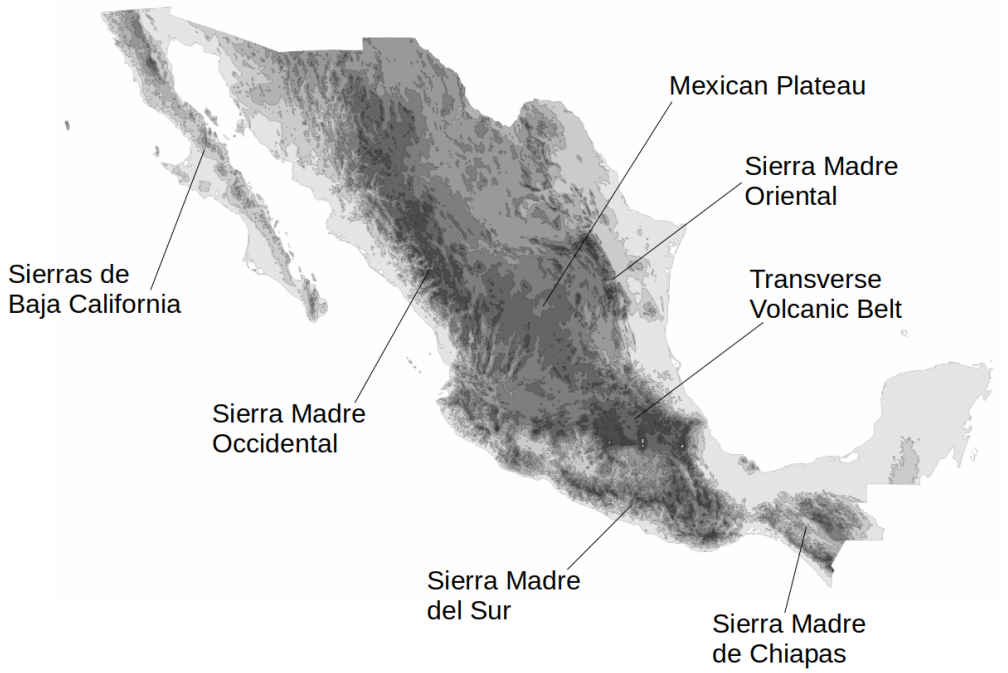


Figure 4.1: Distribution of mountain ranges in Mexico.

Across Mexico, the Transverse Volcanic Belt extends joining the western and eastern mountain ranges with a chain of volcanic mountains reaching heights of 5600 m. Bounded by the Sierra Madre Oriental, Sierra Madre Occidental and the Transverse Volcanic Belt is the Mexican Plateau, altitudes

of reaching 2,000 m. South of the Volcanic Axis, in the west, the Sierra Madre del Sur continues along the Pacific Coast reaching altitudes of 3700 m. On the east, the Sierra Madre Oriental continues and merges with the Sierra Madre del Sur, extending eastward to the Isthmus of Tehuantepec. The Sierra Madre de Chiapas is located east of the Isthmus of Tehuantepec (Perry, 1991).

Species and trait data

Species occurrences were obtained from the Forest and Soils National Inventory of the Mexican Forestry Commission (CONAFOR, 2009) . The National Forest Inventory protocol records trees $\geq$ 7.5 cm diameter at breast height in four 400 m^2 sites, which together form a sampling unit used in this study. Angiosperm records and conifer species not native to Mexico according to Farjon (2010) were excluded. Incomplete records in terms of species name and location, or with geographical coordinates corresponding to locations outside Mexico were also excluded. After data cleaning, 6963 site records were left to be used in the analysis. A total of 198,013 individuals belonging to 70 species representing eight genera and four families, according to APG III (Bremer et al., 2009) were included in the analysis.

A trait matrix was constructed using seven traits of Mexican conifer species extracted from literature descriptions from Farjon (2010) and online databases (Table 4.1). Leaf area was calculated by multiplying the length and width of the leaves, whereas the cone size was measured as the length/width ratio of the cones. Trait data on some of the conifers species was not available, this was the case for wood density on 11 species, bark thickness on four species and seed size data on three species. Trait records absences were included in the analysis as NAs.

Table 4.1: Traits used in the analysis, their main functional role, and sources.

Trait name	Functional role	Source
Height (m)	Fire resistance	Farjon, 2010
Bark thickness (cm)	Fire and pathogen resistance	Farjon, 2010
Wood density (mg/cm^3)	Growth, mechanical strength	Zanne et al., 2009
Seed size (g)	Dispersal and recruitment	Kew Millenium Seed Bank Project
DBH (cm)	Growth rate	Farjon, 2010
Leaf area (cm)	Growth rate	Farjon, 2010
Cone size (cm)	Recruitment	Farjon, 2010

Environmental variables

Maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the warmest quarter and elevation were extracted from the Worldclim database (www.worldclim.org) using the 10 minute resolution (Fick and Hijmans, 2017). These environmental variables (Table 4.2) were used as descriptors of the environmental conditions for the study area. A 0.1 degree grid was used to extract mean values of the environmental variables using the extract function from the raster R package (R Core Team, 2019).

Phylogeny

A phylogenetic tree of Mexican coniferous species was constructed by pruning the age calibrated global conifer phylogenetic tree from Leslie et al. (2012). This phylogeny was generated based on the sequences of four genes, two nuclear genes, 18S and PHYP, and two chloroplast genes, *mat*K and *rbc*L from GenBank. The phylogeny, that samples approximately 80% of

Table 4.2: Environmental variables used in the analysis, minimum, maximum and mean values for the 0.1 degree grid cells.

Environmental variables	Min.	Max.	Mean
Max.T (°C)	14.6	38.21	30.4
Min. T (°C)	-7.2	21.23	5.7
Ann. P (mm)	175	4266	905.5
Summer P. (mm)	17	1046	320
Elevation (m)	156	3715.5	1536.5

Environmental variables are: maximum temperature of the warmest month (Max. T), minimum temperature of the coldest month (Min. T), annual precipitation (Ann. P), precipitation of the warmest quarter (Sum. P) and Elevation.

the extant conifer diversity, with tree cycad genera that were used as an out group, uses a maximum-likelihood tree topology as a constraint topology for inferring the dated phylogeny, and a Bayesian implementation of a relaxed clock model with fossil calibration points as minimum age constraints.

Statistical analysis

Random Forest models

The sites were overlaid on a 0.1 degree grid across Mexico, and a community trait matrix of all the 83 conifer species present in Mexico was generated by calculating the average value per grid cell for each of the seven traits. The environmental relationships of each trait and its geographical distribution were assessed using Random Forest models. Random Forests is a machine learning statistical classifier and an effective tool in prediction that is commonly used in bioinformatics (Cutler et al., 2007). Classification trees have been used by ecologists in recent years, particularly for ecological data mining, because of their simple interpretation, high classification accuracy, and because of their ability to determine variable importance and complex in-

teractions among variables, and they do not assume linearity (Cutler et al., 2007). Random Forests selects bootstrap samples to construct multiple regression trees. A randomised subset of predictors is used to grow each tree, which then are combined into a composite, more accurate model (Cutler et al., 2007; Rueda et al., 2017). The main product of Random Forests is the relative importance of each predictor, assessed by the decrease in the explained variance as a result of permutations of the focal variable (Rueda et al., 2017).

Seven Random Forests models were generated, one for each trait, using the R package RandomForest (Liaw and Wiener, 2002), using the environmental variables as predictors. For each model, 500 regression trees were generated and the percentage of the explained variance was recorded. The importance of each variable was ranked from 100 (strongest predictor) to 0 (least predictive power) and the sign of the relationship was assessed.

Phylogenetic comparative analyses

Niche conservatism in conifer trait was characterised by testing for phylogenetic signal in each trait using Pagel's λ, which assumes a Brownian motion model of trai evolution (Pagel, 1999). A value of $\lambda = 0$ shows that there is no phylogenetic signal in the trait, or that the traits has evolved independently of phylogeny. A value of $\lambda = 1$ indicates that there is strong phylogenetic signal, or that the trait has evolved according to the Brownian motion model of evolution (Kamilar and Cooper, 2013). Phylogenetic generalised least square model (PGLS) was used to test correlations between environment and species traits accounting for phylogeny with mean values of the environmental variables in which each of the species are found across Mexico and their trait values . The PGLS models were performed using the

R package caper (Orme, 2018).

4.3 Results

Out of the seven mapped traits, height, bark thickness, wood density, seed size, leaf area and cone size showed clear geographic patterns across Mexico (Fig. 4.2). The strongest distinction in the trait patterns is between the mountain ranges and the Mexican Plateau. Height, bark thickness, wood density, leaf area and cone size presented higher trait values along the mountain ranges, both Sierra Madre Occidental and Oriental, the Transverse Volcanic Belt, Sierra Madre del Sur, Sierra Madre de Chiapas, and the Northern part of the Sierra de Baja California. Seed size showed a different geographic pattern to the other traits, as conifer seeds tend to have larger values in the Central Mexican Plateau area than in the mountain ranges. Diameter at breast height did not present any evident geographic pattern across Mexico.

Table 4.3: Random forest models for mean trait values of Mexican conifers.

Trait	R^2	Elevation	Max. T.	Min. T.	Ann. P.	Summer P.
Seed size	0.64	32.3 (+)	31.5 (+)	70.0 (-)	**100 (-)**	44.5 (-)
Bark thickness	0.56	37.7 (+)	35.7 (-)	50.0 (+)	**100 (+)**	54.1 (+)
Height	0.53	46.3 (+)	45.4 (-)	60.5 (+)	**100 (+)**	49.9 (+)
Leaf area	0.42	50.0 (-)	45.7 (+)	71.7 (+)	**100 (+)**	63.4 (+)
Wood density	0.31	**100 (-)**	73.3 (+)	**99.2 (+)**	74.4 (+)	60.1 (+)
Cone size	0.30	**95.4 (+)**	89.1 (-)	76.7 (-)	**100 (-)**	71.1 (+)
DBH	0.20	87.9 (-)	80.7 (-)	87.8 (+)	**100 (+)**	76.7 (-)

The most important predictor variables for each trait (>90) are in bold and the sign of the correlation is provided. The traits are ranked by the explanatory power (R^2) of the model. Predictor variables are: maximum temperature of the warmest month (Max. T), minimum temperature of the coldest month (Min. T), annual precipitation (Ann. P), precipitation of the warmest quarter (Sum. P) and Elevation.

Random Forest models show that annual precipitation is the main environmental variable that influences the distribution of traits across Mexico (Table 4.3). Random Forest models found that annual precipitation is positively correlated with bark thickness, height leaf area and diameter at breast height, however it presents a negative correlation with seed size and cone

size. Elevation was positively correlated with cone size and negatively correlated with wood density. Another important predictor variable according to the Random Forest models was minimum temperature, which was positively correlated with wood density.

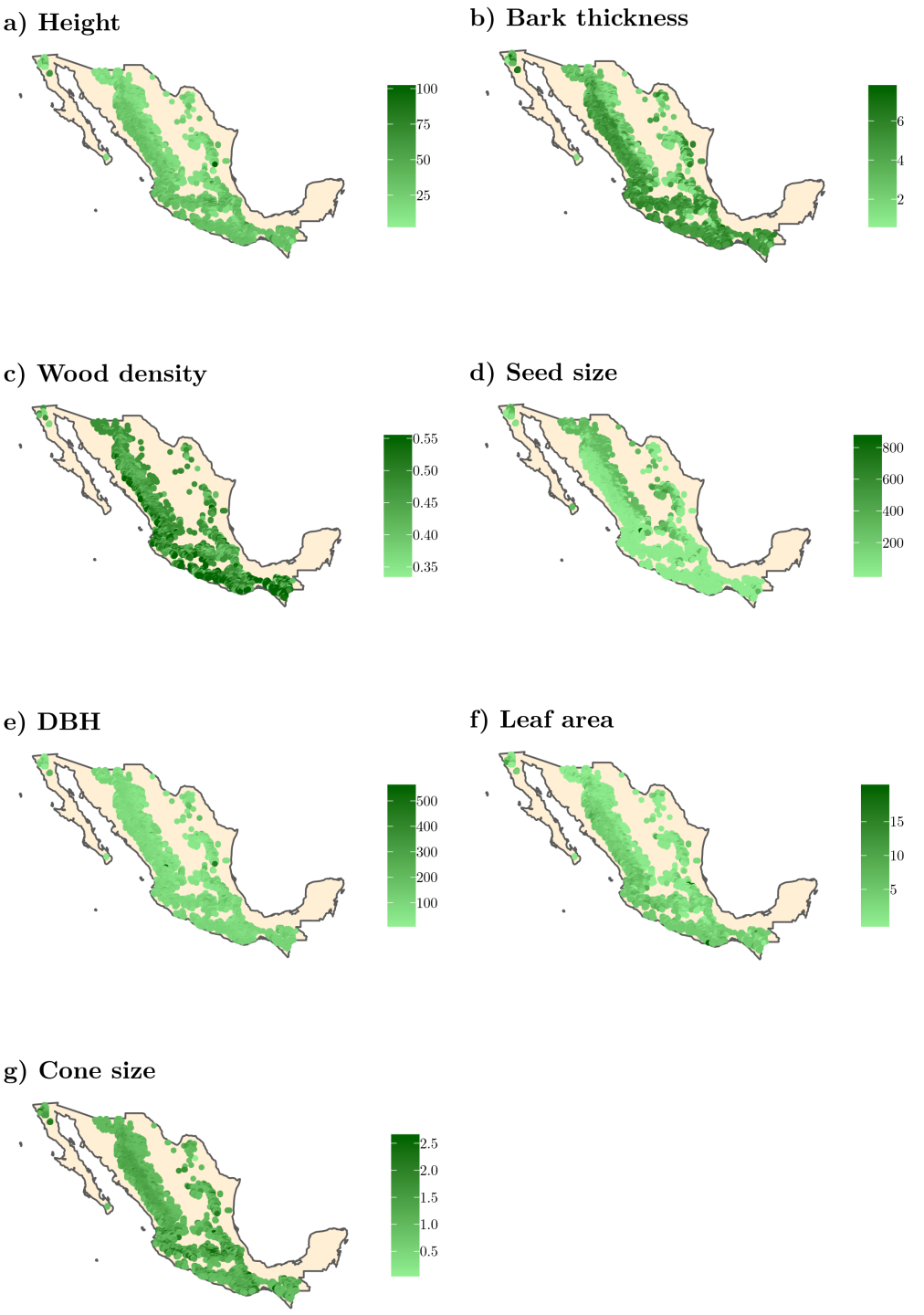


Figure 4.2: Geographical patterns of seven conifer traits across Mexico. The traits are: a) maximum height (m), b)bark thickness (cm), c) wood density (mg/cm^3), d) seed size (gr), e) diameter at breast height (cm), f) leaf area (cm), g)cone size (cm).

Table 4.4: Phylogenetic signal of seven conifer traits using Pagel's lambda.

Trait	λ	95% CI
DBH	0.964	0.909, 0.986
Cone size	0.949	0.824, 0.985
Wood density	0.930	0.813, 0.975
Leaf area	0.923	0.816, 0.972
Height	0.894	0.676, 0.968
Seed size	0.875	0.653, 0.959
Bark thickness	0.632	0.246, 0.887

Conifer traits ranked by decreasing values of λ and their 95% confidence interval is provided.

Phylogenetic signal was strong for all conifer traits (Table 4.4) indicating that that the trait has evolved according to the Brownian motion model of evolution. PGLS models (Table 4.5) showed a positive correlation between DBH and elevation, Leaf area had a positive correlation with minimum temperature of the coldest month, height showed a positive correlation with annual temperature but negative ones with minimum temperature and summer precipitation, bark thickness showed a positive correlation with annual precipitation and a negative one with minimum temperature. Cone size, wood density and seed size did not showed significant correlations to any environmental variable.

Table 4.5: Phylogenetic generalised least squares model explaining the effect of environmental variables on conifer traits.

	DBH	Cone size	Wood density	Leaf area	Height	Seed size	Bark thickness
Intercept	44.713	3.087	0.249	-4.745	12.345	519.167	4.883
Max. T.	2.504	$-2.58\text{x}10^{-2}$	$5.23\text{x}10^{-3}$	0.318	0.410	-12.706	-0.052
Min. T.	-1.847	$7.54\text{x}10^{-3}$	$2.63\text{x}10^{-3}$	**0.265**	**-2.170**	5.517	**-0.213**
Ann. P.	0.062	$-3.03\text{x}10^{-4}$	$-2.52\text{x}10^{-5}$	-0.003	**0.048**	-0.143	$\mathbf{3.86\text{x}10^{-3}}$
Summer P.	-0.151	$-1.08\text{x}10^{-5}$	$9.99\text{x}10^{-6}$	$8.26\text{x}10^{-4}$	**-0.057**	0.110	$4.57\text{x}10^{-3}$
Elevation	**0.052**	$-2.76\text{x}10^{-4}$	$1.62\text{x}10^{-5}$	0.001	$-4.90\text{x}10^{-4}$	-0.023	$3.56\text{x}10^{-4}$

Predictor variables are: maximum temperature of the warmest month (Max. T.), minimum temperature of the coldest month (Min. T.), annual precipitation (Ann. P.), precipitation of the warmest quarter (Summer P.) and Elevation. Predictor variables for each trait with significant values (>95) are in bold.

4.4 Discussion

The purpose of this chapter was to test how environmental variables that act as stressors influence the patterns of conifer traits and the implications for their distribution. Precipitation is the strongest climatic variable explaining the contemporaneous geographical patterns of functional traits and stress tolerances of Mexican conifers. The extreme climatic shifts that conifers have experienced through their evolutionary history have enabled them to occur in environments where several environmental stressors are present, extreme temperature and precipitation in particular (Leslie et al., 2012; Rueda et al., 2017).

Annual precipitation correlates negatively with seed size and cone size. In terms of geographical patterns, seed size shows an increase in size in the Mexican Plateau region, which is characterised by its aridity (Mastretta-Yanes et al., 2015). North American conifers have been reported to present a latitudinal pattern in seed size and to be explained by maximum insolation, which is attributed to the presence of conifers with large seeds in desertic areas (Rueda et al., 2017). Dispersal syndrome in conifers is a known predictor of seed size, as larger seeds that contain more nutrients are dispersed by animals (Leslie et al., 2012). Wind dispersed seeds, which tend to be smaller, are found in species with ancestors from higher latitudes, such as *Abies* and *Picea* (Rueda et al., 2017).

According to the results, wood density is best predicted by elevation and minimum temperature, with a negative and positive correlation respectively. Wood density showed higher values towards the west and south of Mexico. Rueda et al. (2016) found that wood density was lower in boreal forests than in southerns latitudes in North America, where it correlated positively with maximum temperature. In larger-scale studies wood density varies

with latitude, showing similar values in temperate and tropical tree species, but with broader ranges and variances in the latter. In tropical species elevation also appears to have an effect on wood density as it decreases with elevation. However in terms of environmental variables it has been found that wood density increases with temperature and decreases with increasing annual precipitation in angiosperms in tropical sites (Wiemann and Williamson, 2002). High wood density has been correlated with shade tolerance, mechanical strength and resistance to drought induced embolisms (Chave et al., 2009; Kunstler et al., 2016). Wood density and height are often referred as two of the most important traits for plants (Chave et al., 2009; Kunstler et al., 2016). Wood density is used as an indicator of a trade-off between the growth of the plant and its strength, whereas maximum height it indicates a trade-off between the plant's access to light and its early reproduction time (Kunstler et al., 2016).

Leaf area and diameter at breast height were both best predicted by annual precipitation. Leaf area showed a geographical pattern where their highest values are in the mountain ranges, particularly in the Sierra Madre Occidental, the Transverse Volcanic Belt, the Sierra Madre del Sur, and the Sierra Madre de Chiapas. Diameter at breast height, did not present any particular patterns. Šímová et al. (2015) found that leaf area was best explained by temperature in North American trees, and that leaf area geographical pattern exhibited with higher values in the north east.

In the Random Forest models bark thickness and height correlated most strongly with annual precipitation, where its geographical pattern shows that the highest values of bark thickness and height are located in the Mexican mountain ranges. Height has been reported to be correlated with annual precipitation in North American trees (Šímová et al., 2015; Rueda

et al., 2017). There are a number of hypotheses that are used to explain the presence of thick bark in trees, including biotic factors such as protection from pests, mechanical support and protection from extreme environmental conditions such as fires, frost, extreme warmth and droughts (Pausas, 2015). It has been noted that pine species with thick bark are present in warm environments and that boreal species have thinner bark (Keeley, 2012). Bark provides heat insulation and protection from fire, it also protects from water loss in arid environments (Pausas, 2015). Height has also been attributed as an adaptation to fires, as greater height increases the survival to low fires (Rueda et al., 2017).

A common goal of many ecological studies is to explain species diversity patterns, usually with the help of environmental variables. However, the understanding of diversity patterns requires integrating both ecological and evolutionary processes (Kozak and Wiens, 2010). The results of the random forest analysis show that annual precipitation is the strongest environmental variable that explains the geographical patterns of functional traits in Mexican conifers without accounting for the phylogeny of the conifer species. The functional traits included in this chapter exhibited phylogenetic signal that suggests niche conservatism. After analysing environment correlates and species traits while accounting for phylogeny, the results indicate that certain traits show dependency with climate variables even after correcting for phylogenetic relatedness. Diameter at breast height was positively correlated with elevation although, it has been reported to decline with increasing elevation mainly due to a shortening of growing season and to reduction of summer temperatures (Coomes and Allen, 2007). Leaf area was positively correlated to minimum temperature, however, leaf area is usually important because it is a measure of the area available for absorption of solar radiation and for regulating transpiration(Goude et al., 2019).

Conifers height was positively correlated with annual precipitation and negatively with minimum temperature and summer temperature Tree height has shown to be highly plastic especially in species that are broadly distributed as they need to adapt to a range of environmental conditions such as temperature (Wang et al., 2017). Bark thickness serves as protection to fire and high temperatures (Frejaville et al., 2013), conversely the results show a negative correlation between bark thickness and minimum temperature. Cone size, wood density and seed size did not show any correlation with any environmental variable, indicating that these traits have not been influenced by the environment during conifers evolution.

Chapter 5

Species, functional and phylogenetic beta diversity of conifers in Mexican mountain ranges

5.1 Introduction

Biological diversity can be described using three components: alpha diversity (α), beta diversity (β), and gamma diversity (γ) (Whittaker, 1972). Beta diversity is referred to as the species compositional difference between local assemblages (Jost et al., 2011; Yang et al., 2015). Beta diversity can be partitioned in two processes, turnover and nestedness. Turnover results when existent species are replaced by others between sites, whereas nestedness occurs when the species in a given site are a subset of the species present in a richer site (Bishop et al., 2015; Antão et al., 2019; Baselga, 2010). The distinction between the processes responsible for the beta diversity patterns is important for understanding ecological, biogeographical, and conservation questions (Baselga, 2010; Carvalho et al., 2012). This because for conservation purposes, turnover would need the preservation of a large number of sites, independently of their species richness; on the other hand, nestedness would allow for the preservation of a smaller number of sites with the higher richness (Carvalho et al., 2012; Wright and Reeves, 1992).

Turnover of species can be caused by environmental, spatial, and historical factors (Qian et al., 2005; Tuomisto, 2010b), and is considered important because it influences diversity at large scales (Condit et al., 2002). Nestedness patterns originate as a result of sequential colonisations or extinctions along gradients (Ulrich et al., 2009). Tropical tree species turnover has been reported to decline with increasing geographic distance in South American forests (Condit et al., 2002). For pteridophytes and Melastomataceae in the Amazonian forests, floristic similarity decreases with increasing geographic and environmental distance, caused by habitat heterogeneity and dispersal limitation (Tuomisto, 2010b). For eastern North America and eastern Asia, beta diversity of temperate angiosperms is more strongly related to

geographic distance than to climate variables, beta diversity being higher in eastern Asia probably because of the higher environmental heterogeneity (Qian et al., 2005).

Functional and phylogenetic diversity, other than species diversity, may offer a different insight into understanding the drivers of biodiversity patterns. Functional diversity, is associated with current ecological processes, and uses functional traits and the environmental variables to which they are related, whereas phylogenetic diversity gives an indication of the region's biogeographic history, which is likewise associated with the environment (Chun and Lee, 2017). Functional and phylogenetic beta diversity are best predicted by environmental rather than geographic distance in a Chinese tropical forest (Yang et al., 2015). In South Korean mountain ranges, functional and phylogenetic beta diversity decreased with geographic distance, although both functional and phylogenetic beta diversity were more strongly influenced by environmental than geographic distance (Chun and Lee, 2017). In Panama tropical forests, phylogenetic beta diversity is significantly explained by both environmental and geographic distance (Zhang et al., 2013).

Mexico has an unusually high beta diversity of tree species, particularly the areas of the Sierra Madre mountain ranges, due to their sharp environmental gradients and fragmented forests. This also results in low alpha diversity and high gamma diversity (Keil and Chase, 2019). Mexican montane forests contain a high diversity of conifer species, their distribution determined locally by environmental filtering, but also regionally by climatic and geological history. I use mountain ranges in Mexico as study system because of their differences in climatic and geological history, size, climate and topography, allowing complex patterns of species divergence,

speciation, and local persistence to develop (Mastretta-Yanes et al., 2015).

In this chapter I investigated the species, functional, and phylogenetic beta diversity of Mexican conifers across and between eight mountain ranges in Mexico, incorporating species richness, functional traits, and a phylogenetic approach in order to assess the importance of geographic and environmental distance in conifer diversity. I ask the following questions: 1) how are the patterns of species, functional, and phylogenetic beta diversity affected by geographic distance, altitude, and the environmental variables in the mountain ranges; 2) whether geographic distance, altitude or the environment is the most important in shaping beta diversity.

I predicted: (a) an increase in species and phylogenetic beta diversity with increasing geographic distance due to dispersal limitation (Tuomisto, 2010b); (b) an increase in functional beta diversity with environmental distance due to trait selection (Zhang et al., 2016); and (c) that geographical distance would have a weaker impact on functional beta diversity than environmental distance, leading to distinct patterns of turnover.

5.2 Methods

Forest inventory data

Species occurrences were obtained from the Forest and Soils National Inventory of the Mexican Forestry Commission (CONAFOR, 2009) . The National Forest Inventory protocol records trees $\geq$ 7.5 cm diameter at breast height in four 400 m^2 sites, which together form a sampling site used in this study. Angiosperm records and conifer species not native to Mexico according to Farjon (2010) were excluded. Incomplete records in terms of species name and location, or with geographical coordinates corresponding to locations outside Mexico were also excluded. After data cleaning, 6963 site records were left to be used in the analysis. A total of 198,013 individuals belonging to 70 species representing eight genera and four families.

Phylogeny

A phylogenetic tree of Mexican coniferous species was constructed by pruning the age calibrated global conifer phylogenetic tree from Leslie et al. (2012). This phylogeny was generated based on the sequences of four genes, two nuclear genes, 18S and PHYP, and two chloroplast genes, *mat*K and *rbc*L from GenBank. The phylogeny, that samples approximately 80% of the extant conifer diversity, with tree cycad genera that were used as an out group, uses a maximum-likelihood tree topology as a constraint topology for inferring the dated phylogeny, and a Bayesian implementation of a relaxed clock model with fossil calibration points as minimum age constraints.

Species trait information

A trait matrix was constructed using seven traits of Mexican conifer species, extracted from literature descriptions from A. Farjon (2010) and online databases (Table 3.1). Given the nature of the functional beta diversity analysis performed in this chapter, which required for the assemblages to contain more species than traits, principal components analysis (PCA) was used to to reduce trait dimensions (Webb et al., 2010) as variable selection. The first two axes of the PCA explained 51.7% and 47.2% of the variation in the trait dataset respectively (Figure B.1 and B.2). Height, seed size and diameter at breast height were used in the beta diversity analysis as these are the variables that contributed the most to the principal components (Table 5.1).

Table 5.1: Loadings of the variables (traits) for the two most important principal components.

Trait	PC1	PC2
Height	**-0.171596314**	**-0.1385846534**
Bark thickness	-0.010849049	-0.0077072919
Wood density	0.000371907	0.0001030012
Seed size	**-0.425973713**	**0.9031325584**
DBH	**-0.888233525**	**-0.4062640299**
Leaf area	0.002951622	-0.0057916727
Cone size	-0.003969091	-0.0015675947

Loadings that are considered the most important for each principal component are in bold.

Environmental data

Six environmental variables were selected to examine the relationship between the environment and species richness and the indices of functional diversity. Four variables, annual mean precipitation, temperature seasonality, annual precipitation and precipitation seasonality were extracted from

the Worldclim database (www.worldclim.org) using the 5 minute resolution (Fick and Hijmans, 2017). A 0.1 degree grid was used to extract mean values of the environmental variables using the extract function from the raster R package (R Core Team, 2019). Altitude was obtained from the CONAFOR data, at site level. Geographic and environmental distances were calculated as pairwise distances.

Statistical analysis

Pairwise beta diversity

To calculate species, functional and phylogenetic beta diversity, the framework of beta diversity partition by Baselaga (2010) was used. This framework consists on three pairwise beta diversity metrics: βsor or total dissimilarity which accounts for the total compositional variation between assemblages, including turnover and nestedness patterns, βsim or spatial turnover that captures compositional changes due to turnover and βsne that represents the nestedness-resultant dissimilarity, calculated as the difference between βsor and βsim (Bishop et al., 2015). For functional beta diversity, functional dissimilarities calculations are based on the volume of convex hulls intersections in a multidimensional functional space whereas for phylogenetic beta diversity, functional dissimilarities are based on Faith's phylogenetic diversity (Baselga et al., 2018). Only species, functional and phylogenetic total beta diversity was analysed and reported.

The relationships between species, functional and phylogenetic beta diversity and the environmental distances were described using generalised linear models (GLMs) with a binomial distribution. Model simplification was performed by dropping terms starting off from a full model that included all explanatory variables, the models AIC was used to infer which variables are

the most important. (Crawley, 2005). All analyses were performed using R programming language (R Core Team, 2019).

5.3 Results

Species beta diversity (Table 5.2) in its total dissimilarity component is mainly influenced by annual mean temperature and annual precipitation, total dissimilarity increases with the difference in annual temperature and annual precipitation (Fig. 5.1). Functional beta diversity has as important variables geographic distance and the difference in annual precipitation (Table 5.3). Functional beta diversity as total dissimilarity increased with both geographic and precipitation distance (Fig. 5.2). Phylogenetic beta diversity on its total dissimilarity component has as strong factors temperature seasonality and annual precipitation (Table 5.4). Phylogenetic beta diversity as total dissimilarity increased with the difference in temperature seasonality and precipitation (Fig. 5.3)

Table 5.2: Model selection for the effect of geographic distance, altitude and environmental variables on species beta diversity as total dissimilarity. Predictor variables are: geographical distance (geodist), altitude (alt), annual mean temperature (amt), temperature seasonality (ts), annual precipitation (ap), precipitation seasonality (ps).

Model	Resid. Df	Resid. Dev	dAIC	weight
Total dissimilarity				
geodist + alt + amt + ts + ap + ps	4561697	1553257.99	0.00	1.00
geodist + alt + amt + ts + ap	4561698	1564063.88	7574.40	0.00
geodist + alt + amt + ts + ps	4561698	1593481.61	43601.10	0.00
geodist + amt + ts + ap + ps	4561698	1561953.16	7300.60	0.00
geodist + alt + ts + ap + ps	4561698	1587451.04	69415.90	0.00
geodist + alt + amt + ap + ps	4561698	1553464.82	1525.00	0.00
alt + amt + ts + ap + ps	4561698	1590894.55	35242.30	0.00

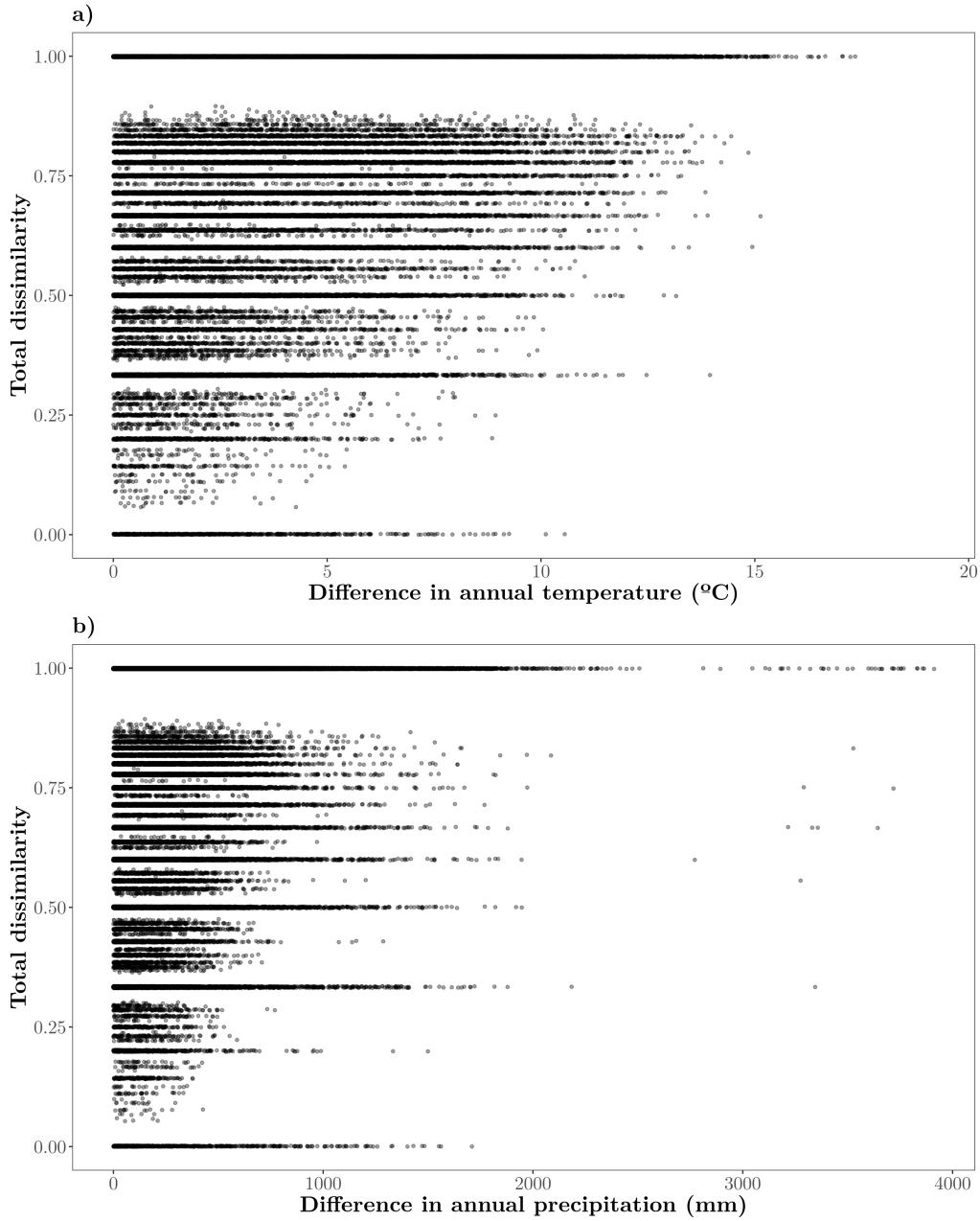


Figure 5.1: Relationship between species beta diversity as total dissimilarity and the most important predictor variables, a) Difference in annual temperature and b) Difference in annual precipitation.

Table 5.3: Model selection for the effect of geographic distance, altitude and environmental variables on functional beta diversity as total dissimilarity. Predictor variables are: geographical distance (geodist), altitude (alt), annual mean temperature (amt), temperature seasonality (ts), annual precipitation (ap), precipitation seasonality (ps).

Model	Resid. Df	Resid. Dev	dAIC	weight
Total dissimilarity				
geodist + alt + amt + ts + ap + ps	262443	92448.27	0.00	1.00
geodist + alt + amt + ts + ap	262444	92585.41	360.80	0.00
geodist + alt + amt + ts + ps	262444	94530.19	3589.60	0.00
geodist + amt + ts + ap + ps	262444	93402.90	1532.50	0.00
geodist + alt + ts + ap + ps	262444	93927.52	1679.10	0.00
geodist + alt + amt + ap + ps	262444	93335.42	586.60	0.00
alt + amt + ts + ap + ps	262444	98508.34	4633.20	0.00

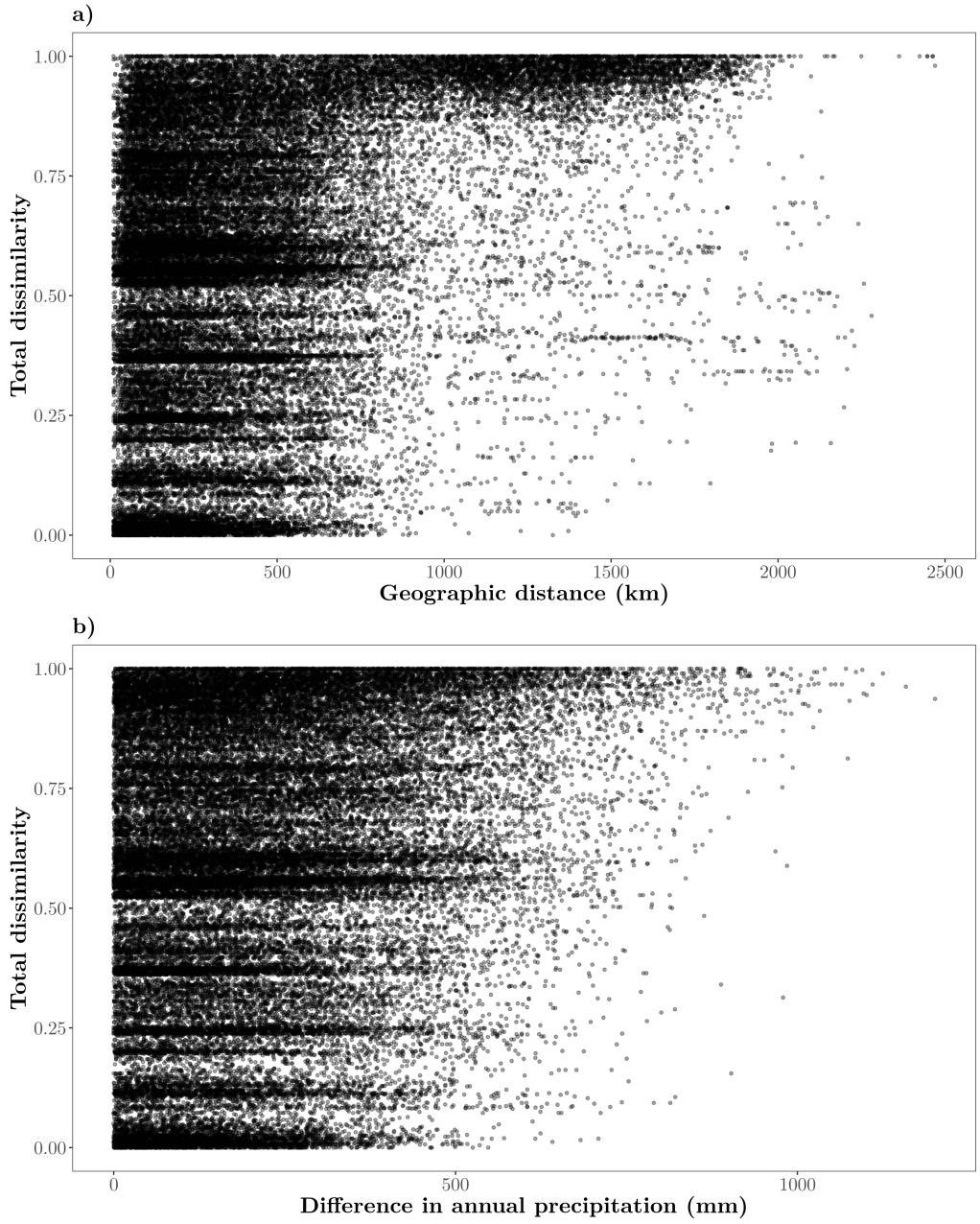


Figure 5.2: Relationship between functional beta diversity as total dissimilarity and the most important predictor variables, a) Geographic distance and b) Difference in annual precipitation.

Table 5.4: Model selection for the effect of geographic distance, altitude and environmental variables on phylogenetic beta diversity as total dissimilarity. Predictor variables are: geographical distance (geodist), altitude (alt), annual mean temperature (amt), temperature seasonality (ts), annual precipitation (ap), precipitation seasonality (ps).

Model	Resid. Df	Resid. Dev	dAIC	weight
Total dissimilarity				
geodist + alt + amt + ts + ap + ps	4561697	1617239.34	8301.80	0.00
geodist + alt + amt + ts + ap	4561698	1624122.69	16857.10	0.00
geodist + alt + amt + ts + ps	4561698	1623527.58	18343.40	0.00
geodist + amt + ts + ap + ps	4561698	1620087.28	14974.80	0.00
geodist + alt + ts + ap + ps	4561698	1618050.39	0.00	1.00
geodist + alt + amt + ap + ps	4561698	1657832.76	36907.70	0.00
alt + amt + ts + ap + ps	4561698	1621096.12	11658.50	0.00

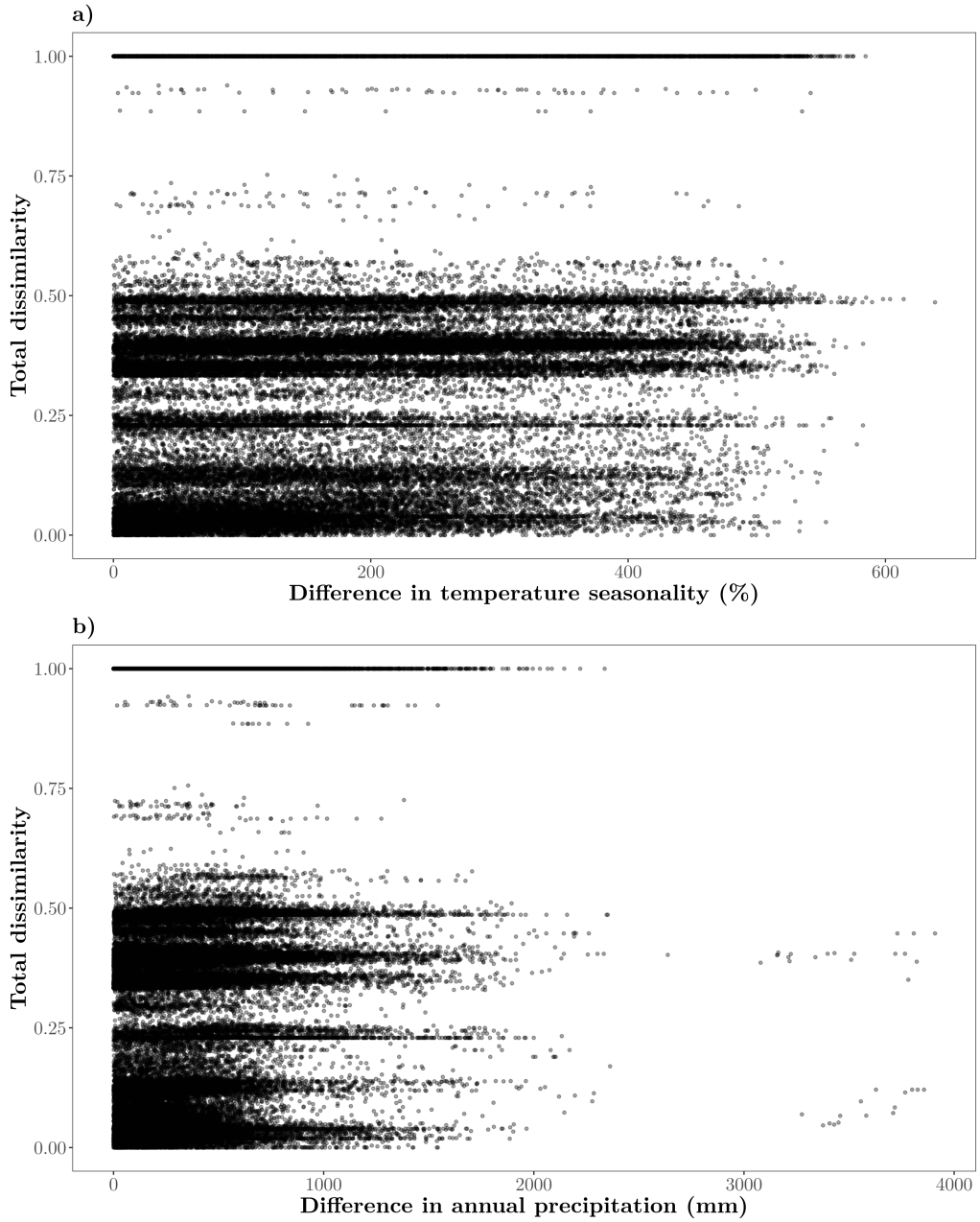


Figure 5.3: Relationship between phylogenetic beta diversity as total dissimilarity and the most important predictor variables, a) Difference in temperature seasonality and b) Difference in annual precipitation.

5.4 Discussion

The aim of this chapter was to investigate the patterns of species, functional and phylogenetic beta diversity across Mexican forests and how beta diversity is influenced by geographic and environmental distance. I found that conifers beta diversity is mainly influenced by environmental distance rather than by geographic distance.

I predicted an increase in species and phylogenetic beta diversity with increasing geographic distance due to dispersal limitation. The results show that species beta diversity as total dissimilarity is mainly influenced by annual mean temperature and annual precipitation and that species total dissimilarity increases with the difference in both temperature and precipitation. These results agree with Tuomisto (2010) who found that environmental determinism explains the floristic differences between sites rather than dispersal limitation. However, geographic distance has been reported as an important factor in species turnover in shrubs in northeastern China, this pattern was explained by dispersal limitation. Species beta diversity has been reported to increase with increasing precipitation in grasslands in Mongolia (Zhang et al., 2014a). Phylogenetic beta diversity was mainly influenced by environmental distances. Temperature seasonality and annual precipitation were the most important factors; total dissimilarity was found to increase with both environmental distances. Similarly to my results, phylogenetic beta diversity has been reported to be better explained by environmental distance in tropical tree communities in Panama (Zhang et al., 2013).

Other predictions were that functional beta diversity will increase with environmental distance due to trait selection and that functional beta diversity will be better explained by environmental distance rather than biographic

distance. I found that both Geographic distance and environment distance as annual precipitation were the most important factors influencing functional beta diversity. Total dissimilarity was found to increase with both geographic distance and annual precipitation. Yang et al. (2015) found that functional and phylogenetic beta diversity are better explained by environmental distance than by geographic distance across spatial scales; this pattern was attributed to a rapid turnover in lineages and functions in the forest terrain, which presented rapid changes in topography and environment in short spatial distances.

Overall, the environment seems to be the most important factor in shaping beta diversity. However, both geographic and environmental distance play important roles in shaping species, functional and phylogenetic beta diversities.

A key limitation of this chapter is the concern of pseudoreplication because of the pairwise distances lack of independence where a single community is involved in multiple comparisons, therefore results for this chapter should be cautiously interpreted. Another limitation of this chapter is the methodological approach used proposed by Baselaga (2010) and that has been criticised in spite of being considered as an important contribution for being a partitioning framework whose components reflect the underlying mechanisms driving beta diversity (Podani and Schmera, 2016). This framework proposes a partitioning of beta diversity into two components: spatial turnover and nestedness. However it has been criticised because the partitioning of the beta diversity components does not follow an algebraic decomposition into additive components measured on the same scale (Schmera and Podani, 2011). One of the main criticism has been to the nestedness component as it does not fit the requirements to be considered

as a true nestedness-resultant dissimilarity, but instead it only quantifies how the differences in species richness that are not due to species replacement contribute to patterns of beta diversity along spatial or environmental gradients (Almeida-Neto et al., 2012). There has been a surge in metrics for measuring beta diversity, each with its own merits and difficulties, in spite its criticisms, for this chapter I chose this framework because of its partitioning approach, although only total beta diversity was reported.

There is a debate as to which statistical approach to analyse beta diversities is the most suitable. Tuomisto (2010) revised several methodological approaches for the analysis of beta diversity, following either a regional approach where the effective species turnover is quantified in a dataset resulting in a single value per dataset or with a pairwise approach, useful when investigating the variation of beta diversity and how is affected by the environment. The pairwise approach for quantifying beta diversity uses beta diversity values for different subsets of the data forming pairwise combinations leading to a dissimilarity matrix where the minimum value is zero when the pair of sampling units are compositionally identical (Tuomisto, 2010a). Several analysis use dissimilarity matrix for beta diversity computations such as: distance-based redundancy analysis, a constrained ordination method which assess the effect of explanatory variables and is suitable for phylogenetic and ecologic distances; generalised dissimilarity model, a technique for modelling spatial variation of diversity based on the variation in environmental conditions, such as distances and predicting the change in communities composition based on a curvilinear relationship with the predictor variables (Ferrier et al., 2007); hierarchical or agglomerative clustering, a clustering analysis where single variables that are most similar to each other are joined in a separate node, which are then joined with other nodes until all variables are combined in nodes belonging to a single

cluster, the result is presented as a dendrogram or heat map where colour gradients or the connectivity and length of the branches reflect the similarity between variables and nodes (Shankar and Paliy, 2016); and mantel test, which tests the correlation between distance matrices while accounting for the non-independence of the observations by a randomisation method to test for significant correlations between matrices (Kanaroglou and Delmelle, 2016). This overview of statistical techniques for the analysis of beta diversity brings to light perhaps more suitable alternatives for the analysis of this chapter that would address its main limitations. Ultimately the choice of analysis method to address beta diversity will depend on the type of data available, the type of dissimilarity distance that was constructed, the presence of null values and the question that needs to be answered.

Chapter 6

Conclusions

This thesis sought to understand how the diversity of conifers in Mexico has been generated and the mechanisms through which diversity is maintained. My research aimed to answer how the different types of conifer diversity is influenced by environmental drivers in Mexico.

Firstly, I explored the extent to which environmental drivers act as filters to regulate species and functional diversity of conifers in Mexico. I found that species richness and functional diversity are influenced by environmental drivers in different ways. However there was a consistent positive effect from the interaction of temperature and precipitation on both species richness and functional diversity. It was unexpected to find that temperature and precipitation seasonality do not necessarily limit species richness and functional diversity.

Then I analysed how the distribution of conifers is driven by environmental stressors and the phylogenetic conservatism of conifer traits. The results showed that the most important environmental variable that explains the geographical patterns of conifer functional traits is annual precipitation. In terms of the geographic distribution of the traits, I found that they showed higher values in mountain areas, with the exception of seed size. The func-

tional traits exhibited phylogenetic signal suggesting niche conservatism.

Finally I investigated species, functional and phylogenetic beta diversity of conifers across Mexico and assessed how environmental and geographic distance influence beta diversity patterns. Environmental distance appears to have a stronger influence in shaping beta diversity. However beta diversity patters show complex interactions between geographic distance and environmental differences making beta diversity challenging to be explained by a single variable.

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Appendix A

Table A.1: List of conifer species recognised by the National Forest Inventory 2004-2009 (CONAFOR The National Forestry Commission of Mexico, 2009)

Specie	Number of individuals
Abies concolor	25
Abies durangensis	95
Abies hickelii	155
Abies hidalgensis	30
Abies religiosa	3649
Abies vejarii	11
Cupressus arizonica	733
Cupressus guadalupensis	143
Cupressus lusitanica	2715
Juniperus blancoi	1
Juniperus californica	34
Juniperus coahuilensis	305
Juniperus comitana	7
Juniperus deppeana	19626
Juniperus durangensis	594
Juniperus flaccida	3666
Juniperus jaliscana	14
Juniperus martinezii	153
Juniperus monosperma	1497
Juniperus monticola	184
Juniperus pinchotii	81
Juniperus saltillensis	13
Picea chihuahuana	48
Pinus arizonica	14198
Pinus attenuata	15
Pinus ayacahuite	5477
Pinus caribaea	1
Pinus cembroides	21670
Pinus cooperi	4084
Pinus coulteri	3
Pinus culminicola	5
Pinus devoniana	2356
Pinus douglasiana	4452
Pinus durangensis	27860
Pinus engelmannii	7576
Pinus flexilis	1
Pinus greggii	507
Pinus hartwegii	1338
Pinus herrerae	4484
Pinus jaliscana	169
Pinus jeffreyi	155
Pinus lambertiana	7
Pinus lawsonii	1365

Pinus leiophylla	12626
Pinus lumholtzii	9305
Pinus luzmariae	73
Pinus maximartinezii	35
Pinus maximinoi	1038
Pinus monophylla	77
Pinus montezumae	1592
Pinus nelsonii	101
Pinus oocarpa	14777
Pinus patula	2780
Pinus pinceana	350
Pinus ponderosa	31
Pinus praetermissa	400
Pinus pringlei	1535
Pinus pseudostrobus	7834
Pinus quadrifolia	417
Pinus radiata	44
Pinus remota	278
Pinus rzedowskii	6
Pinus strobiformis	1844
Pinus strobus	209
Pinus tecunumanii	19
Pinus teocote	12079
Podocarpus guatemalensis	4
Podocarpus matudae	70
Pseudotsuga menziesii	963
Taxodium huegelii	24

Appendix B

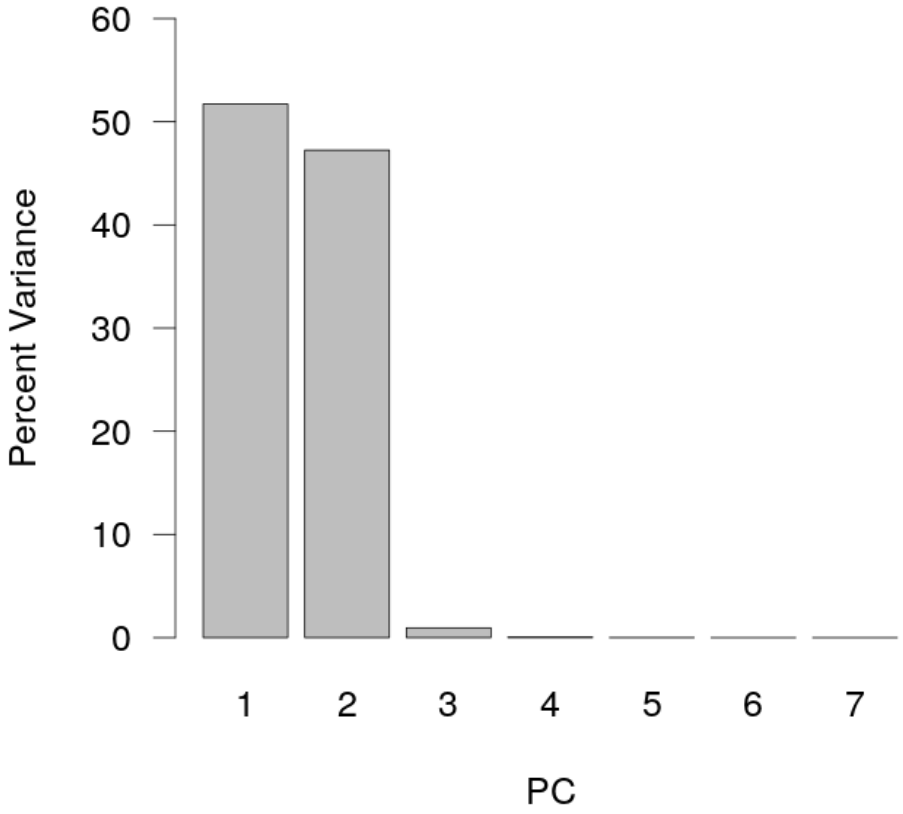


Figure B.1: Scree plot that shows the explained variance of each of the principal components of the principal component analyses (PCA).



Figure B.2: Ordination diagram of the two first axes of principal component analyses (PCA).