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# Vegetation Structure, Classification and Climatic Characteristics in Temperate-like Mountain Forests Dominated by *Abies jaliscana* in Western Mexico

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**Abstract**

*Aim of study*: Examine patterns in woody species composition, vegetation structure, precipitation and temperature parameters over two fir forest elevation ranges and to discuss some biome-climate characteristics.

*Area of Study*: Field sampling was conducted in 20 *Abies* forest sites over two elevation ranges (Laguna Juanacatlan and Cerro La Bufa) in western Jalisco, Mexico.

*Material and Methods*: Using linear regressions, relationships between climate and fir forest structure were inferred. We examined vegetation structure complemented by cluster and indicator species analyses.

*Main results*: A total of 2378 stems belonging to 67 species were recorded, species richness and Shannon index were not different between localities. Cluster analysis suggest three forest types: upper montane cloud forest (UMCF), mixed fir-UMCF and fir forest. Fir basal area and abundance showed differences between localities. Reverse J-shaped size distribution pattern was found, except in the Cerro La Bufa lower belt, where a J-shaped pattern indicates low recruitment and high number of canopy individuals.

*Highlights*: The lower temperatures and increase in winter rainfall along the elevational gradient, enable an auspicious habitat for western Mexican fir forests.

**Keywords***:* *Abies jaliscana*, Forest Structure, Precipitation of Coldest Quarter, Fir Forest Subtypes, Temperate-like Biome

# Meksika'nın Batısındaki Abies jaliscana'nın Egemen Olduğu Ilıman Ormanların Bitki Örtüsü Yapısı, Sınıflandırılması ve Iklimsel Özellikleri

**Öz**

*Çalışmanın Amacı:* Farklı yükseltilerdeki iki farklı göknar ormanının odunsu türlerinin kompoziyonunun, vejetasyon yapısının, yağış ve sıcaklık parametreleri bakımından incelenmesi ve bazı biyom-iklim özelliklerini tartışmak.

*Çalışma Alanı:* Alan örneklemesi, Meksika'nın batı Jalisco kentinde iki yükseklik aralığında (Laguna Juanacatlan and Cerro La Bufa) seçilmiş yirmi farklı Abies ormanında yapılmıştır.

*Materyal ve Yöntem:* Doğrusal regresyonlar kullanılarak, iklim ve göknar ormanlarının yapısı arasındaki ilişkiler ortaya çıkarılmıştır. Küme ve gösterge türlerinin analizleri ile tamamlanan bitki örtüsünün yapısı incelenmiştir.

*Sonuçlar:* 67 türe ait toplam 2378 birey kaydedilmiş olup, tür zenginliği ve Shannon indeksine göre bölgeler arasında farklılık gözlenmemiştir. Kümeleme analizi üç orman türü önermektedir: yüksek dağ ormanı, karışık göknar yüksek dağ ormanı ve göknar ormanı. Göknar bazal alanı ve bolluğu bölgeler arasında farklılıklar göstermiştir. Bir J-şekilli desenin işaret ettiği düşük stok ve yüksek sayıda kanopi bireyini gösteren Cerro La Bufa'nın alt kısımları haricinde, ters J-şekilli boyut dağılım modeli bulunmuştur.

*Önemli vurgular:* Düşük sıcaklıklar ve yükselti gradyanları boyunca artan kış yağışları, Meksika göknar ormanları için iyi bir yaşam alanı sağlamaktadır.

**Anahtar kelimeler:** Abies jaliscana, Orman Yapısı, En Soğuk Çeyreğin Yağışları, Göknar Ormanı Alt Türleri, Ilıman Benzeri Biyom

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## Introduction

The distribution, diversity and structure of plant communities are strongly driven by climate (Holdridge, 1947; Stephenson, 1990; Peinado et al., 2012). Human impact and other environmental conditions such as physiographical, biological, and edaphic factors also play an important role (Olvera-Vargas, Figueroa-Rangel & Vázquez-López, 2010; Linares, Carreira & Ochoa, 2011). Vegetation science, based on size data and classification is a valuable tool that attempt to understand the forest structure, the establishment, development and the complex mosaic of different plant communities.

Mountain fir forests represent an ideal ecosystem for ecological research, particularly the study of the relationship between vegetation and climate. Fir forests structure has been widely studied in boreal (Kneeshaw and Bergeron, 1998; Antos and

Parish, 2002), mediterranean (Arista, 1995) and temperate regions (Pauley and Clebsch, 1990; Cogbill and White, 1991). In subalpine belts from North America and Asia, *Abies lasiocarpa* (Hook.) Nutt., *A. fargesii* Franch., *A. georgei* var. *smithii* (Viguié & Gaussen) C.Y. Cheng, W.C. Cheng & L.K. Fu and *A. spectabilis* Mirb. have been studied in terms of community structure, population dynamics and growth shifts (Whittaker and Niering, 1975; Dang, Zhang, Zhang, Jiang & Zhang, 2010; Liang, Wang, Xu, Liu & Shao, 2010; Gaire, Koirala, Bhuju & Borgaonkar, 2014; Chhetri, Bista & Cairns, 2016; Shrestha, Chhetri & Bista, 2017). Other fir species in the western United States have been analyzed structurally, e.g. *Abies magnifica* A.Murray in California (Taylor and Halpern, 1991), *A. concolor* (Gordon & Glend.) Lindl. ex Hildebr. and *A. nobilis* A. Dietr. in Oregon (Whittaker, 1960).

Mexican firs are influenced by tropical and mediterranean macrobioclimate (Peinado, Bartolomé, Delgadillo & Aguado, 1994; Giménez de Azcárate and Ramírez, 2004; Giménez de Azcárate, Macías-Rodríguez & Gopar-Merino, 2013), but due to their temperate and boreal affinity, they are restricted to high mountain zones with low temperatures. Therefore, this high elevation distribution compensates the lack of long and intense winters in tropical and subtropical latitudes (Rzedowski, 1978). Furthermore, these forests are relicts of a more extended distribution during the late Miocene (Graham, 1999); currently, the genus in Mexico probably grows at the threshold of its ecological and climatic requirements and needs cool microhabitats with high humidity. Moreover, this condition makes them more vulnerable to global climate change.

In Mexico, there are several studies on structural analysis, but very few descriptive ones about floristic composition (Sánchez-González, López-Mata & Vibrans, 2006; Encina-Domínguez, Encina-Domínguez, Mata-Rocha & Valdés-Reyna, 2008; Cuevas-Guzmán et al., 2011; Guerrero-Hernández, González-Gallegos & Castro-Castro, 2014). Furthermore, there is a lack of studies, mainly in subtropical and tropical latitudes, which classify fir forest subtypes and examine changes in temperature and precipitation in relation to elevation, which in turn could correspond with changes in fir forest structure. Only Ávila, Aguirre & García (1994) analyzed environmental variables in relation to structure in Pico de Orizaba, Veracruz, Mexico, recognizing four physiognomic types (*Abies hickelii-Pinus ayacahuite-P. patula* forest, *A. hickelii-P. pseudostrobus* forest, *A. hickelii* monospecific forest and *A. hickelii-Alnus jorullensis* forest) of fir forest, however the temperature was measured for a very short period of time (10 days) and precipitation was overlooked.

We focused on relict forests with restricted distribution in climatic refugia, remaining from a wider distribution at the Miocene and middle Pliocene (Aguirre-Planter et al., 2012), such as those dominated by our target species, *Abies jaliscana* (Martínez) Mantilla, Shalisko & A.Vázquez, which exhibits a remarkably isolated distribution in the western Mexican cloud forests (Guerrero-Hernández et al., 2014), *Upper Montane Cloud forests sensu* Ohsawa (1995). This fir species is locally abundant, is distributed only in steep coastal mountains and humid ravines from Jalisco (western Mexico), mainly on seaward and north-facing slopes at 1800–2400 m a.s.l., it has only been recorded in five areas on the western Trans-Mexican Volcanic Belt (TMVB) and the extreme northwestern range of the Sierra Madre del Sur, in the Pacific

Basin (Vázquez-García, Shalisko, Cuevas-Guzmán, Muñiz-Castro & Mantilla-Blandón, 2014). On the other hand, Velázquez, Toledo & Luna (2000) state that fir forests in Mexico occur on very steep to moderate slopes at 2800–3500 m elevation.

In this study, we examine patterns in woody species composition, vegetation structure, and separately, analyze changes in precipitation and temperature over two narrow ranges of elevation at two areas with fir forest in western Jalisco, Mexico. Our specific aims were to (1) examine patterns in the structure of vegetation and woody species composition of the *A. jaliscana* forests from western Mexico (2) characterize fir population structure and asses differences between populations, and (3) look at changes in precipitation and temperature along elevation ranges and to discuss some biome-climate characteristics for fir forests.

## Materials and methods

*Tree species*

*Abies jaliscana* is a relict species belonging to the section *Grandis*, in a group from western Mexico which includes *A. flinckii* Rushforth and *A. durangensis* Martínez. *A. jaliscana* was previously known as *A. guatemalensis* Rehder var. *jaliscana* Martínez (1948); however Rushforth (1989) included this variety in *A. flinckii* populations, until Vázquez-García et al. (2014) provided morphological, phenological and geographical evidence to support the recognition of the western populations as a distinct species.

*Study Area*

This study was conducted in two locations at the north limit distribution of *A. jaliscana*: Laguna Juanacatlan (J), with the highest elevation at 2420 m, 55 km from the Pacific Ocean; mainly exposed to the windward inland slopes, and Cerro La Bufa (B), with the highest elevation at 2600 m, 40 km from the ocean; mainly exposed to the coast slopes. These sites are located in the western region of Jalisco state, Mexico, near the Pacific Ocean coast. The study area is located in the Trans-Mexican Volcanic Belt western slopes where it overlaps with the northern limit of Sierra Madre del Sur, in western Mexico (Figure 1). The origin of these mountains is the result of intermediate mafic volcanism, covering the late Pliocene to the Quaternary (Gómez-Tuena, Orozco-Esquivel & Ferrari, 2005). The soils have been classified as Andosols; the texture is sandy loam with high cation exchange capacity and high organic matter content (Guerrero-Hernández, 2016). The nearest meteorological station is located in the town of San Sebastian del Oeste at 1403 m a.s.l., which registered an annual mean temperature of 18.8 °C and total annual precipitation of 1354.7 mm in 38 years (SMN, 2017). Nevertheless, at the lower and upper belts of the study area, mean annual temperature values are 16.6 and 13.2 °C respectively, and the annual precipitation ranges from 1228 mm in the lower sites to 1183 mm in the upper sites, according to the downloaded bioclimatic data from WorldClim (Hijmans, Cameron, Parra, Jones & Jarvis, 2005). As a comparative reference, a weather station was installed in the *Abies* forest stand J2374 (2374 m a.s.l.) for one year (2014–2015) and the annual mean temperature was 13.6 °C. Additionally, the meteorological station from the town of Mascota, Jalisco (12 km SW from Juanacatlan locality) was checked to verify the bioclimatic data from WorldClim. The localities were selected by the dominance of *A. jaliscana* in fir forests and upper montane cloud forests along the altitudinal range in which thrives, from 1750 to 2450 m, in two areas separated by *Pinus-Quercus* forests. Other criteria for selection of study sites were that they were old-growth forests with a good state of forest conservation, without evident or known human disturbances. However, in Cerro La Bufa locality a moderate level of disturbance was inferred, according to the presence of light demanding plant species in a few sites. The frequency and intensity of human disturbances as extensive cattle ranching, forest fires and logging are low or absent in the study sites.

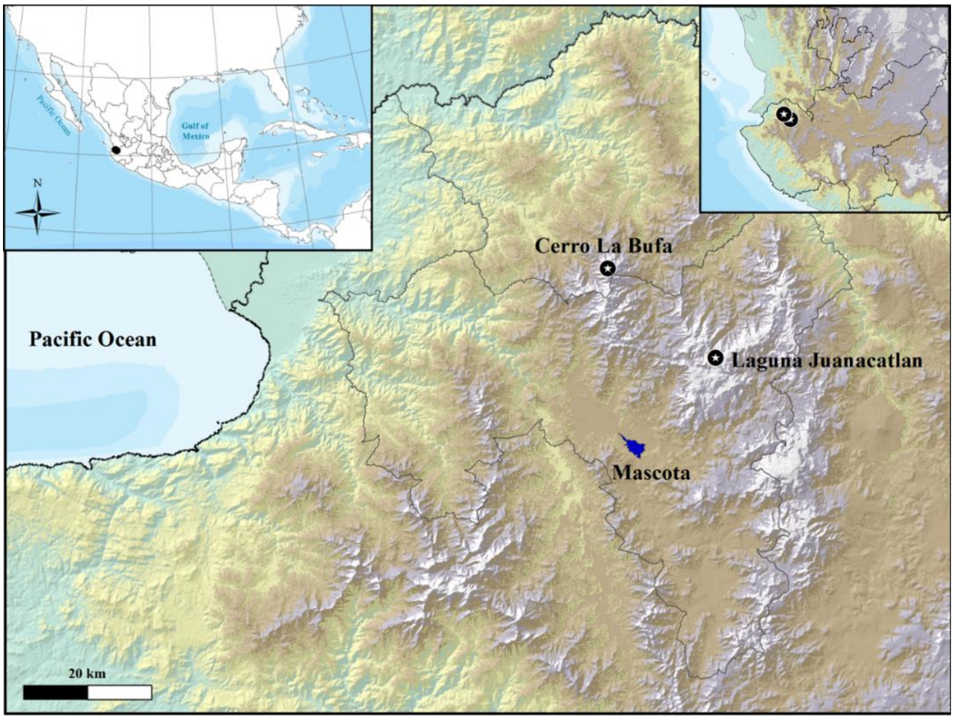


Figure 1. Northern distribution area and the two study localities of *Abies jaliscana* forests in western Mexico. Stars in a black circle indicate study sites.

*Field Sampling*

We used a stratified random sampling design, following Vázquez and Givnish (1998). After an extensive field reconnaissance, a total of 20 sites (ten forest stands per locality) were selected and located on windward slopes at two localities with fir forest remnants. The stands were established at Laguna Juanacatlan (2100–2413 m a.s.l.), and Cerro La Bufa (1755–2447 m a.s.l.) near to the summit (2600 m elevation) (Table 1) (Figure 2). Within each site (0.1 ha, 60 × 48 m area, subdivided in a grid of 12 × 12 m squares) we randomly selected 10 out of 20 circular plots (each 0.01 ha and centered at each square), five from each of the two strata (upper and lower half of the grid). Within these circular plots all woody individuals ≥ 2.5 cm in DBH (ca. 1.3 m) were measured and identified at species level. Growth-form (tree, shrub or vine) was also recorded for each species. Fertile specimens were collected as vouchers and deposited in the IBUG herbarium, at Universidad de Guadalajara, Mexico.

Table 1. Characteristics of the studied *Abies jaliscana* sites in western Jalisco, Mexico.

| Site | N Latitude | W Longitude | Elev. (m) | Slope (°) | Aspect (°) | AP (mm) | T mean (°) | PCQ (mm) | S |
|---|---|---|---|---|---|---|---|---|---|
| **Cerro La Bufa** | | | | | | | | | |
| 1 | 20°44'55.7" | 104°49'30" | 1750 | 25 | 327 | 1228 | 16.6 | 73 | 20 |
| 2 | 20°44'42.2" | 104°49'13.1" | 1970 | 19 | 315 | 1215 | 15.1 | 79 | 18 |
| 3 | 20°44'39.2" | 104°49'11.6" | 2020 | 33 | 315 | 1215 | 15.1 | 79 | 17 |
| 4 | 20°44'33.3" | 104°49'9.1" | 2102 | 29 | 315 | 1215 | 15.1 | 79 | 14 |

*Table 1. (Continued)*

| Site | N Latitude | W Longitude | Elev. (m) | Slope (°) | Aspect (°) | AP (mm) | T mean (°) | PCQ (mm) | S |
|---|---|---|---|---|---|---|---|---|---|
| **Cerro La Bufa** | | | | | | | | | |
| 5 | 20°44'17.2" | 104°49'35.2" | 2170 | 32 | 270 | 1220 | 14.7 | 82 | 11 |
| 6 | 20°43'50.3" | 104°49'47.6" | 2265 | 35 | 358 | 1217 | 13.2 | 89 | 10 |
| 7 | 20°44'2.2" | 104°48'52.4" | 2282 | 20 | 10 | 1215 | 14.5 | 79 | 13 |
| 8 | 20°43'47.5" | 104°49'43.1" | 2345 | 31 | 341 | 1217 | 13.2 | 89 | 9 |
| 9 | 20°43'51.7" | 104°49'38.9" | 2374 | 37 | 315 | 1217 | 13.2 | 89 | 12 |
| 10 | 20°43'43.6" | 104°49'37.7" | 2447 | 29 | 329 | 1217 | 13.2 | 89 | 13 |
| **Laguna Juanaca-tlan** | | | | | | | | | |
| 1 | 20°37'15.5" | 104°43'11.3" | 2100 | 28 | 317 | 1200 | 15.1 | 77 | 18 |
| 2 | 20°36'45.8" | 104°41'59" | 2170 | 32 | 292 | 1188 | 14.3 | 80 | 14 |
| 3 | 20°36'58.9" | 104°41'42.3" | 2256 | 31 | 297 | 1188 | 14.3 | 80 | 17 |
| 4 | 20°36'58.1 | 104°41'50.4" | 2280 | 21 | 280 | 1188 | 14.3 | 80 | 16 |
| 5 | 20°36'57.2" | 104°41'42.1" | 2298 | 18 | 250 | 1188 | 14.3 | 80 | 12 |
| 6 | 20°36'33.2 | 104°42'5" | 2353 | 23 | 280 | 1193 | 14.6 | 79 | 13 |
| 7 | 20°37'48.4" | 104°42'2.2" | 2360 | 28 | 280 | 1187 | 13.8 | 83 | 15 |
| 8 | 20°37'36.6 | 104°42'3.7" | 2374 | 10 | 160 | 1187 | 13.8 | 83 | 9 |
| 9 | 20°37'48.1" | 104°41'48.4" | 2401 | 12 | 225 | 1183 | 13.9 | 81 | 10 |
| 10 | 20°37'46.9" | 104°41'43.1" | 2413 | 12 | 100 | 1183 | 13.9 | 81 | 10 |

Geographical coordinates, elevation, slope, aspect, annual precipitation (AP), annual mean temperature (T mean), precipitation of coldest quarter (PCQ) and species richness (S)

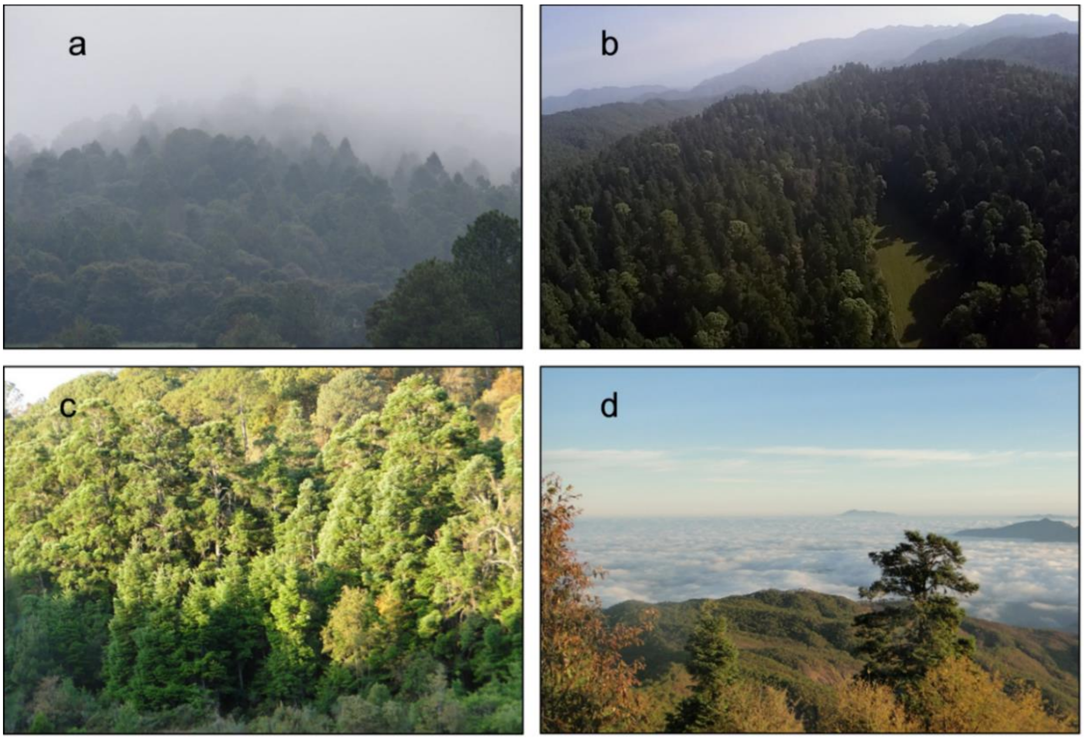


Figure 2. Landscape and stands pictures of Cerro La Bufa-Juanacatlan in western Jalisco, Mexico. (a) Fog incidence in a stand of Laguna Juanacatlan; (b) monospecific fir forest in Laguna Juanacatlan; (c) stand B2282 in Cerro La Bufa with high disturbance in the forest margins; (d) orographic cloud rising in Cerro La Bufa.

Climate information included the original 19 bioclimatic variables downloaded from the WorldClim database (Hijmans et al., 2005) for each site. The cell values from the rasters of the bioclimatic variables were obtained by the use of the “sample raster values” algorithm of Q-GIS program v. 2.18 (QGIS Development Team, 2018), using the point layer corresponding to the geographical coordinates of the sampling sites. No preprocessing or other derivation procedure was needed for the WorldClim bioclimatic layers. The precipitation of the warmest quarter, precipitation of the coldest quarter of the year, annual mean temperature and annual precipitation were selected using stepwise regression analysis and Pearson correlation, employing SIGMAPLOT V.11.0 (Systat Software Inc., 2008). These four climatic variables were selected instead of their correlated variables, being that several authors consider them as key variables for climate-vegetation relationships (Whittaker, 1975; Hijmans et al., 2005; Williams-Linera, Toledo-Garibaldi & Gallardo-Hernández, 2013; Toledo-Garibaldi and Williams-Linera, 2014). The precipitation of the warmest quarter and precipitation of the coldest quarter of the year are two important variables for plant survival and growth in tropical montane forests with high seasonality (Goldsmith, Matzke & Dawson, 2013; Gotsch et al., 2014; Allen, Kirchner, Braun, Siegwolf & Goldsmith, 2019).

WorldClim could not be the optimal data source to describe climatic variability in small spatial scales but certainly, it is the climate system with more precision all over the world (Hijmans et al., 2005). In addition, WorldClim was created by interpolating processes that include Anusplin methods which take into account the generation of smoothed surfaces of parameters (including precipitation); in these processes an elevation adjustment is considered, thus extrapolation of precipitation data is regulated by elevational values, ensuring the best possible estimation of precipitation for high sites even for those lacking a meteorological station

*Data Analysis*

Species richness (S), Shannon Diversity Index (H', natural log), fir basal area ($m^2$/ha) and density (stems/ha) were calculated as descriptive measures of the woody community for each site. The Shannon Index and species richness were computed using EstimateS ver. 9.1.0 (Colwell, 2015). Statistical analyses for differences in mean values of such variables were performed using a t-test in SIGMAPLOT 11.0 (Systat Software Inc. 2008) with a level of significance $\alpha = 0.05$. Additionally, basal area and stem density were calculated per species within each stand. Fir trees were grouped into size classes at 10 cm intervals according to DBH in each site, the height of the trees was divided into six vertical strata: 1(1.3–10 m), 2 (11–20 m), 3 (21–30 m), 4 (31–40 m), 5 (41–50 m), 6 (51–56 m), and both DBH and vertical stratification was averaged by altitudinal belts. To assess changes in precipitation, temperature and fir basal area along elevation ranges, we fitted linear regressions between the independent variable x (elevation in our study) and the dependent variable y (climate variables and basal area in our study). The annual precipitation and annual mean temperature values that characterize the limit between the coniferous and the tropical upper montane cloud forest zones were examined using Holdridge life's zones (1947) and Whittaker biomes (1975).

Hierarchical agglomerative cluster analysis (McCune and Grace, 2002) was used to determine groups of sampling sites. This analysis was carried out using Sorensen (Bray-Curtis) distance measurements with the beta flexible linkage (beta = -0.25), which is the clustering linkage method of choice to avoid staggered groups. Indicator species analysis (ISA) was used as a quantitative, objective criterion to prune the dendrogram resulting from the hierarchical clustering. ISA yields an indicator value (between 0 and 1) with its statistical significance using a Monte Carlo technique based on 1,000 randomizations. Differences in species composition among groups of sites were tested with a multiresponse permutation procedure (MRPP). When all the species within groups are identical, the within-group agreement statistic $A$ reaches its maximum value ($A$ = 1); when the heterogeneity within groups equals the level expected by chance, then $A$ = 0, and when there is more heterogeneity within groups than the level expected by chance, then $A < 0$. In MRPP a $p$ value is given for each test group comparison. Classification and statistical tests were performed using the PC-ORD v. 6.0 software (McCune & Grace, 2002).

## Results

*Woody Species Composition*

A total of 2378 stems belonging to 67 species were recorded in 20 sites (2 ha); the genus *Quercus* was predominant with 10 species. The total species richness was higher in Cerro La Bufa (55 species) than in Laguna Juanacatlan (34 species), however, the estimated mean species richness (S, $t$ = -0.19902, $P > 0.05$) and Shannon index (H', $t$ = -1.92711, $P > 0.05$) were not statistically different between localities (Figure 3c-d). The most frequent species were *A. jaliscana* (20 sites), *Clethra hartwegii* (10 sites), *Meliosma dentata* (7 sites), *Oreopanax xalapensis* (8 sites), *Ostrya virginiana* (8 sites), *Quercus calophylla* (7 sites), *Q. castanea* (9 sites), *Q. obtusata* (14 sites), *Styrax argenteus* (10 sites) and *Symplocos citrea* (8 sites) (Appendix). The plots with less tree species richness in Laguna Juanacatlan were recorded at the highest elevations (sites 8, 9 and 10), whereas in Cerro La Bufa were the sites 6 and 8 (Table 1).

*Classification*

The cluster analysis dendrogram based on species presence-absence in the sites was cut at a scale of 55% of remaining information, clustering sites in six groups (Figure 4); the homogeneity within groups was higher than the expected by chance (MRPP, $T$ = -6.91, $A$ = 0.31, $p < 0.001$). The first group included upper montane cloud forest sites located at the lowest elevations (sites 1–3 at Cerro La Bufa, B1750, B1970, B2020); the second, third, fourth and sixth groups included mixed fir forest-upper montane cloud forest (sites 4, 5, 6, 7, 8, 9 and 10 at Cerro La Bufa; sites 1, 2, 3, 4, 6 and 7 at Laguna Juanacatlan). In contrast, one fraction of the fifth group included the most monospecific *Abies*-dominated forests (5, 8, 9 and 10 at J) (Figure 4). The ISA identified ten species as strong indicators of the groups ($p < 0.05$) (Table 2).

From indicator species and classification analysis, forests were named based on two criteria, the first criterion is to name forests subtypes based on species dominants and in the second criterion we used the Ohsawa nomenclature (Ohsawa, 1991; 1995) for tropical montane cloud forests:

*Upper montane cloud forest zone* (group 1), at 1750–2020 m a.s.l. Evergreen species mixed with deciduous trees; evergreen elements such as *Magnolia pacifica*, *Symplococarpon purpusii*, *Inga hintonii* and *Symplocos citrea* were found in subcanopy and understorey. The deciduous elements were represented by *Carpinus caroliniana*, *Ostrya virginiana*, *Quercus centenaria* (González-Villarreal, 2018) and *Quercus nixoniana*. The canopy was dominated by *Abies*, *Carpinus* and *Magnolia*.

*Mixed fir forest-upper montane cloud forest zone* (groups 2, 3, 4, one fraction of group 5 and 6, plots J2100, J2170, J2256, J2280, J2353, J2360, B2170, B2265, B2282, B2345, B2374 and B2447), at 2100–2450 m a.s.l. In this zone, canopy was dominated extensively by *A. jaliscana*, which reach heights of > 50 m. Despite the high dominance of fir trees, there was a well-developed understorey in different layers represented by species such as *Arbutus xalapensis*, *Clethra hartwegii*, *Cleyera integrifolia*, *Ilex tolucana*, *Meliosma dentata*, *Myrsine juergensenii*, *Ostrya virginiana*, *Quercus obtusata*, *Symplocos citrea*, *Styrax argenteus* and *Ternstroemia lineata*.

*Coniferous forest zone* (*Abies* forest; one fraction of group 5, plots J2998, J2374, J2401, J2413), at 2300–2420 m a.s.l. The coniferous forest zone was exclusively dominated in each layer by one conifer, i.e., *A. jaliscana*, although in the understorey, some trees with small sizes of the genera *Pinus*, *Prunus*, *Quercus* and *Styrax* were found. In this forest zone, *Abies* reached up to 53 m in height and 1.45 m DBH.

Table 2. Indicator species (in bold) and fir forest groups determined by cluster analysis and indicator species analysis.

| Species | Maximum indicator value | *P* |
|---|---|---|
| Group 1 | | |
| ***Ageratina areolaris*** | **0.745** | **0.0284** |
| ***Clethra fragans*** | **1** | **0.003** |
| *Magnolia pacifica* | 0.542 | 0.6415 |
| *Miconia albicans* | 0.791 | 0.0614 |
| ***Quercus centenaria*** | **0.853** | **0.0098** |
| ***Rumfordia floribunda*** | **0.661** | **0.0496** |
| ***Xylosma flexuosa*** | **0.853** | **0.0104** |
| Group 2 | | |
| *Quercus gentryi* | 0.674 | 0.2 |
| *Quercus scytophylla* | 0.674 | 0.1194 |
| Group 3 | | |
| ***Quercus martinezii*** | **0.853** | **0.0108** |
| *Telanthophora jaliscana* | 0.503 | 0.3319 |
| Group 4 | | |
| *Cupressus lusitanica* | 0.674 | 0.2002 |
| ***Quercus crassifolia*** | **1** | **0.0112** |
| Group 5 | | |
| *Pinus leiophylla* | 0.5 | 0.163 |
| *Prunus serotina* | 0.504 | 0.1666 |
| ***Quercus castanea*** | **0.692** | **0.0006** |
| ***Quercus obtusata*** | **0.354** | **0.0422** |
| ***Styrax argenteus*** | **0.598** | **0.0008** |
| Group 6 | | |
| *Cleyera integrifolia* | 0.535 | 0.146 |
| *Meliosma dentata* | 0.593 | 0.0854 |
| *Oreopanax xalapensis* | 0.535 | 0.1538 |
| *Symplocos citrea* | 0.535 | 0.1476 |

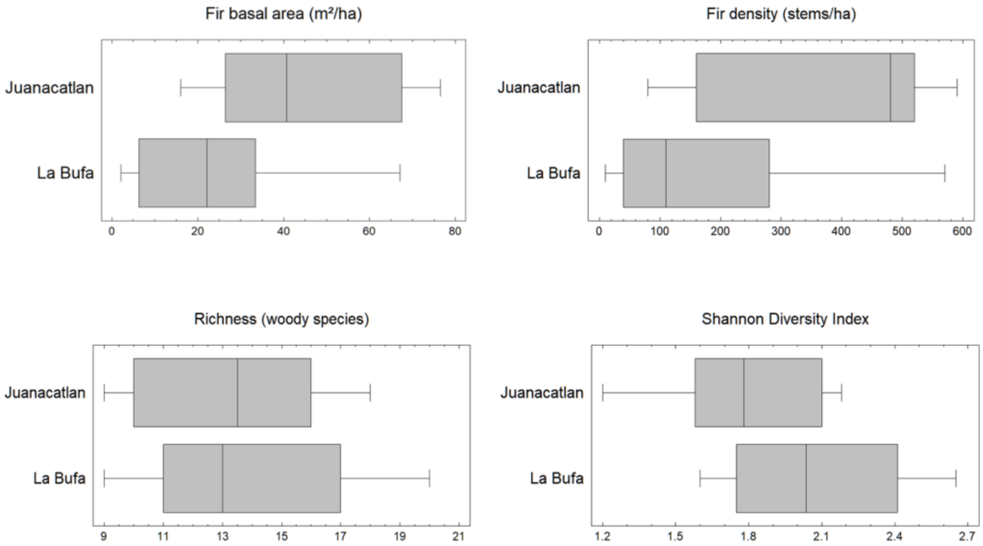


Figure 3. Box plots of basal area (a), stem density (b), species richness (c) and Shannon diversity index (d), of fir population per locality. Boxes depict standard deviation of the mean (filled circles); lines depict 95% confidence interval; Cerro La Bufa (B) and Laguna Juanacatlan (J).

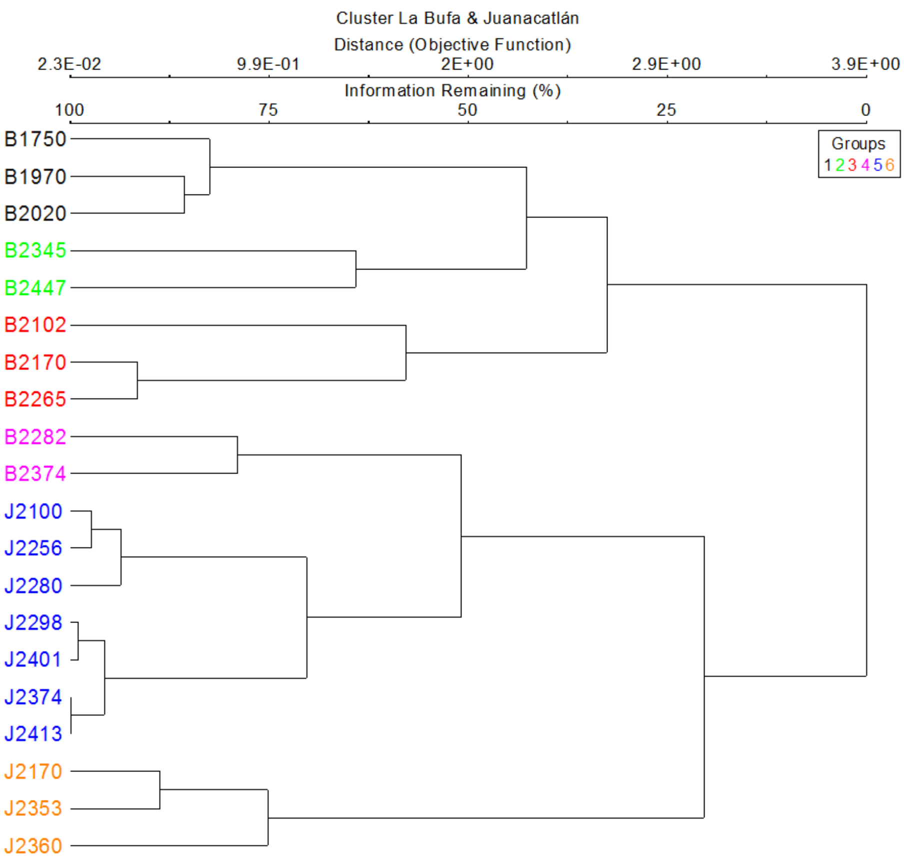


Figure 4. Cluster analysis dendrogram of the study sites between 1750 and 2447 m a.s.l. in fir forests of western Jalisco, Mexico, using Sorenson distance and beta flexible (-0.25) linkage method, cut at 50% of the remaining information scale. Cerro La Bufa (B) and Laguna Juanacatlan (J)

*Fir Forest Structure*

In both localities, *A. jaliscana* exhibited the highest basal area followed by *Quercus castanea*, *Q. centenaria*, and *Q. obtusata*. Likewise, *A. jaliscana* showed the highest abundance followed by *Clethra hartwegii*, *Styrax argenteus* and *Symplocos citrea* (Table 3). Basal area of the fir population was higher in Laguna Juanacatlan than in Cerro La Bufa (BA, $t$ = 2.40, $P$ = 0.027; Figure 3a); fir tree density also showed significant differences between locations (N, $t$ = 2.19, $P$ = 0.042), being higher in Laguna Juanacatlan (Figure 3b). The $DBH_{max}$ in Laguna Juanacatlan was 1.45 and in B was 1.15 m; likewise, the maximum values for height were 56 and 50 m at localities Laguna Juanacatlan and Cerro La Bufa, respectively. The fir diameter distributions within the studied forest are shown in Figures 5a-b. The fir population in Laguna Juanacatlan showed a reverse J-shaped distribution pattern at each elevation (lower and upper belts). At the lower belt, there was a higher proportion of individuals in the first categorycompared to those in the last category (Figure 5a). The upper belt had lower recruitment, higher survival in size classes 2, 3 and twice as old individuals than the lower belt (Figure 5a). In contrast, in Cerro La Bufa, the lower belt showed low recruitment and survival with a high number of old individuals (J-shaped pattern). The middle and upper elevations showed a reverse J-shaped distribution pattern, but the middle belt showed more individuals in the last class than the other belts (Figure 5b). In Cerro La Bufa's upper belt, the small fir trees (DBH < 10 cm) accounted for 35.7% of the total population of fir trees, whereas in Laguna Juanacatlan they represented only the 26.4%. Regarding large trees (DBH > 70 cm), there was a lower proportion in Cerro La Bufa (4.1%) compared to Laguna Juanacatlan (11.5%).

The height distribution in Laguna Juanacatlan showed a reverse J-shaped pattern (multiage population) in both elevational belts (Figures 5c-d). In contrast, the canopy trees in Cerro La Bufa at the lower belt had the higher proportion with 57.1% (J-shape), than the middle belt, which showed a reverse J-shaped distribution pattern, the saplings (1.3–10 m height) had the highest percentage of occurrence (43.1%) in the middle belt. In the upper belt, the first and second stratum exhibited 40.1 and 34.7% of the individuals respectively, and the rest of strata had the least amount of stems. In the study area, fir basal area exhibits a slight increasing trend in relation to elevation ($R^2$ = 0.23, $P$ = 0.033) (Figure 6). In summary, basal area, tree density, height and DBH varied among the different elevational belts in both localities (Table 4).

*Climatic Characteristics*

In both localities, annual precipitation values are over 1100 mm and the highest elevation sites exhibited annual mean temperature values (AMT) below 14 °C (Table 1). The AMT did not show significant differences between the two localities (Mann-Whitney $U$ = 45.5, $P$ = 0.74) and the annual precipitation was higher in Cerro La Bufa than in Laguna Juanacatlan (Mann-Whitney $U$ = 0.00, $P$ < 0.001). In both localities, the AMT had a decreasing monotonic pattern in relation to elevation (Figures 7a-b).

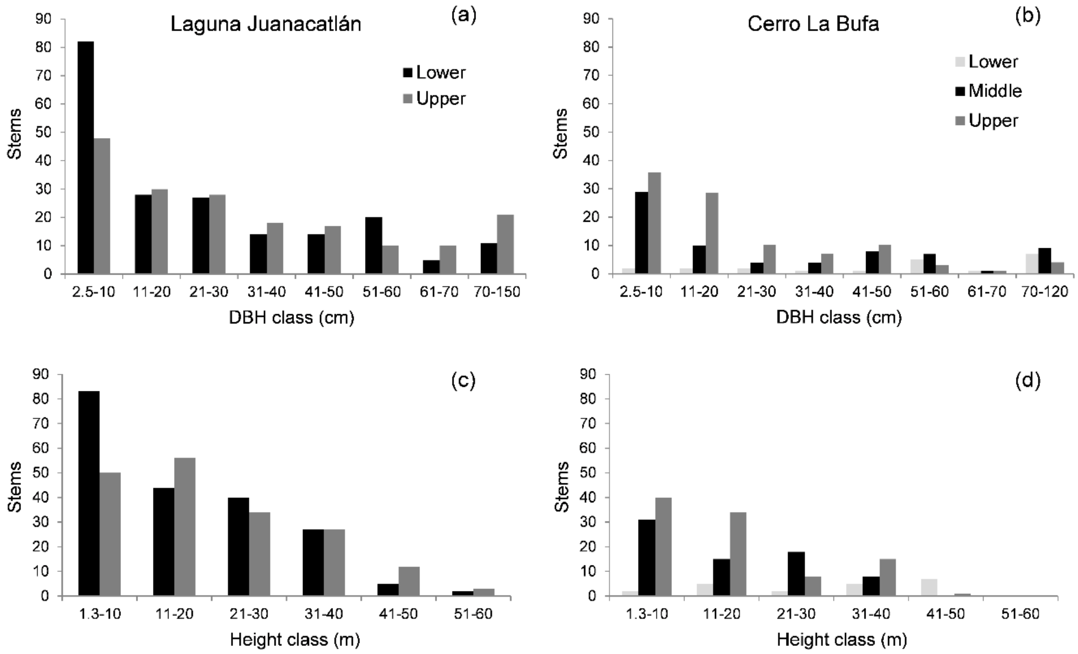


Figure 5. Size class distribution (DBH) of the fir trees at different elevation belts in Laguna Juanacatlan (a) and Cerro La Bufa (b) in western Jalisco, Mexico. Size class: 1 = 2.5–10 cm, 2 = 11–20 cm, 3 = 21–30 cm, 4 = 31–40 cm, 5 = 41–50 cm, 6 = 51–60 cm, 7 = 61–70 cm, 8 > 70 cm. Height class distribution of the fir trees at different elevation belts in Laguna Juanacatlan (c) and Cerro La Bufa (d) in western Jalisco, Mexico. Height stratum: 1 = 1.3–10 m, 2 = 11–20 m, 3 = 21–30 m, 4 = 31–40 m, 5 = 41–50 m, 6 = 51–60 m. Y-axis shows the total number of stems per locality and elevational belt.

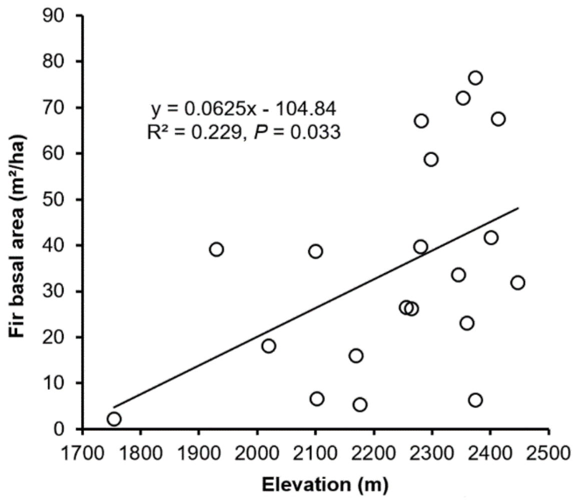


Figure 6. Scatterplot of fir basal area along elevation range for 20 stands in western Mexico.

Table 3. Tree species composition of the fir (*A. jaliscana*) forests in western Jalisco, Mexico.

| Species | Density (stems/ha) | Basal area ($m^2$/ha) | Relative density (%) | Relative basal area (%) |
|---|---|---|---|---|
| **Laguna Juanacatlan** | | | | |
| *Abies jaliscana* | 383 | 46.04 | 26.62 | 68.93 |
| *Quercus obtusata* | 60 | 4.57 | 4.17 | 6.84 |
| *Quercus castanea* | 28 | 2.2 | 1.95 | 3.3 |
| *Pinus pseudostrobus* | 14 | 2.18 | 0.97 | 3.26 |
| *Clethra hartwegii* | 110 | 2.04 | 7.64 | 3.05 |
| *Arbutus xalapensis* | 30 | 1.8 | 2.08 | 2.69 |
| *Symplocos citrea* | 88 | 1.36 | 6.12 | 2.04 |
| *Styrax argenteus* | 394 | 0.96 | 27.38 | 1.43 |
| *Pinus oocarpa* | 5 | 0.88 | 0.35 | 1.31 |
| *Ostrya virginiana* | 14 | 0.8 | 0.97 | 1.19 |
| Other 24 species | 313 | 3.98 | 21.75 | 5.96 |
| Totals | 1439 | 66.81 | 100 | 100 |
| **Cerro La Bufa** | | | | |
| *Abies jaliscana* | 191 | 23.6 | 20.34 | 52.07 |
| *Quercus centenaria* | 61 | 4.13 | 6.5 | 9.11 |
| *Clethra hartwegii* | 46 | 2.77 | 4.9 | 6.12 |
| *Quercus martinezii* | 39 | 2.12 | 4.15 | 4.68 |
| *Quercus scytophylla* | 15 | 1.48 | 1.6 | 3.27 |
| *Arbutus xalapensis* | 12 | 1.24 | 1.28 | 2.72 |
| *Quercus obtusata* | 20 | 1.14 | 2.13 | 2.51 |
| *Ostrya virginiana* | 51 | 1.11 | 5.43 | 2.46 |
| *Quercus rugosa* | 20 | 1.04 | 2.13 | 2.29 |
| *Meliosma dentata* | 4 | 0.59 | 0.43 | 1.31 |
| Other 45 species | 480 | 6.1 | 51.11 | 13.46 |
| Totals | 939 | 45.32 | 100 | 100 |

The annual precipitation occurred without significant changes along the elevational range in Cerro La Bufa, but in Laguna Juanacatlan a decreasing trend was detected ($P = 0.015$) (Figure 7d) and the precipitation of the warmest quarter in Cerro La Bufa decreased ($P < 0.001$) regarding elevation (Figure 7c). In contrast, the precipitation of the coldest quarter had a significant increase along the elevational range in both localities. Maximum temperature of warmest month and minimum temperature of coldest month were highly correlated with annual mean temperature; therefore they were excluded from the results.

The climatic parameters of these forests were examined using Holdridge life's zones. Sites at both localities are located in the warm temperate moist forest zone (annual mean temperature = 13.2–16.6 °C, annual precipitation = 1183–1217 mm) (Table 1), and some of the highest elevation stands thrive relatively near to the cool temperate belt. Only one low-altitude plot (co-dominant species *Magnolia pacifica*, *Quercus centenaria* and *Pinus douglasiana*) exhibited annual mean temperature values above 16 °C, near to the limit of the subtropical-warm temperate belts (18 °C); the rest of the sites had *Abies*-microphyllous-notophyllous trees forest (with understory species as *Clethra hartwegii*, *Ilex tolucana*, *Meliosma dentata*, *Ostrya virginiana*, *Styrax argenteus* and *Symplocos citrea*, 15.1–14.0 °C) and *Abies* monospecific forest (14.5–13.8 °C).

## Discussion

Fir forests from western Mexico mix with broadleaved tropical montane cloud forest in the lower and middle belts of their altitudinal distribution (Vázquez-García, Vargas–Rodríguez & Aragón, 2000; Cuevas-Guzmán et al., 2011). In this study we have documented an interesting replacement from the tropical upper montane evergreen microphyllous forests (e.g. indicator elements such as *Ilex*, *Meliosma*, *Myrsine* and *Symplocos*) to "humid temperate conifer" forest towards higher elevations. This replacement has also been observed in montane forests of south Mexico, western Guatemala and Southeast Asia (Hartshorn, 1988; Ohsawa, 1995). It is important to mention that pines and oaks also thrive in the canopy, subcanopy and understorey, a pattern found by other researchers in the west, center and northeast of Mexico in fir forests (Sánchez-González et al., 2006; Encina-Domínguez et al., 2008; Cuevas-Guzmán et al., 2011).

The cluster analysis dendrogram shows that groups 4 and 5 are very similar because of the high abundance of fir individuals. However, some of the highest elevation plots J2374, J2401 and J2413 (8, 9 and 10 respectively, group 5) had the lowest woody species richness in Laguna Juanacatlan and the highest basal area for *Abies*; they also tend to be nearly monospecific forests. These attributes coincide with the findings by Arista (1995), Ávila et al. (1994) and Cuevas-Guzmán et al. (2011) in high elevation stands where other fir species occur. In contrast, in Cerro La Bufa there was a peak with the highest fir basal area and abundance at 2282 m a.s.l. (plot B2282), above that elevation there was a decrease in basal area (in plots B2345, B2374 and B2447). A similar result was reported by Dang et al. (2010) on *Abies fargesii* in the Qinling Mountains, China. Some authors have identified this trend in peaks above 3500-3600 m a.s.l. at the TMVB, where the precipitation, species richness, fir basal area and stem density decline abruptly towards higher elevations (Sánchez-Velásquez, Pineda-López & Hernández-Martínez, 1991; Sánchez-González and López-Mata, 2003; Toledo- Garibaldi & Williams-Linera, 2014). This trend could be attributed to lower moisture conditions, very low atmospheric pressure and lower temperatures above that elevational level, which might be a limiting factor for firs. However, in Cerro La Bufa, this trend was unexpected since western Mexican firs do not reach these altitudinal levels because there are not mountains higher than 3000 m in the region. Furthermore, it is notable the higher density and basal area for *A. jaliscana* in the upper belt elevation in Laguna Juanacatlan, while in Cerro La Bufa a higher dominance was observed in the middle belt (Table 4). A peculiarity in Cerro La Bufa was the high abundance of heliophilous species, such as *Ageratina areolaris*, *Roldana angulifolia* and *Rumfordia floribunda*, which suggests high disturbance likely due to an anthropogenic origin and an abrupt relief, with slopes greater than 30 degrees in five plots (Table 1). We found significant differences in basal area and density of fir populations between the two locations, being Laguna Juanacatlan the one with the higher values in both structural variables. This result was not expected either, because Cerro La Bufa has a wider elevational range, higher amount of rainfall and it is located slightly closer to the ocean that Laguna Juanacatlan (Table 1, Figure 1 and Figure 8); this water availability and high humidity, in theory, would facilitate the presence, growth and biomass production of fir forest (Toledo-Garibaldi & Williams-Linera, 2014). A possible explanation is that the natural reservoir at Laguna Juanacatlan might play an important role in a better development of fir trees; however, further studies will be necessary to assess that hypothesis.

Table 4. Structural characteristics of *A. jaliscana* population at different altitudinal belts in Cerro La Bufa and Laguna Juanacatlan in western Jalisco, Mexico. ± symbol indicates standard deviation; DBH is diameter at breast height; BA is basal area.

| Altitudinal belt | Elevation(m) | DBH (cm) | BA ($m^2$/ha) | Density (stems/ha) | Height (m) |
|---|---|---|---|---|---|
| **Cerro La Bufa** | | | | | |
| Lower belt | 1750–2000 | 52.76 ± 1.33 | 19.76 | 70 | 30.90 ± 6.69 |
| Middle belt | 2100–2300 | 30.40 ± 7.14 | 26.26 | 180 | 16.52 ± 2.58 |
| Upper belt | 2300–2449 | 21.87 ± 4.28 | 23.89 | 326.66 | 15.89 ± 2.01 |
| **Laguna Juanacatlan** | | | | | |
| Lower belt | 2100–2300 | 24.69 ± 3.20 | 35.91 | 402 | 17.78 ± 1.67 |
| Upper belt | 2300–2413 | 33.03 ± 4.33 | 56.18 | 364 | 20.91 ± 1.84 |

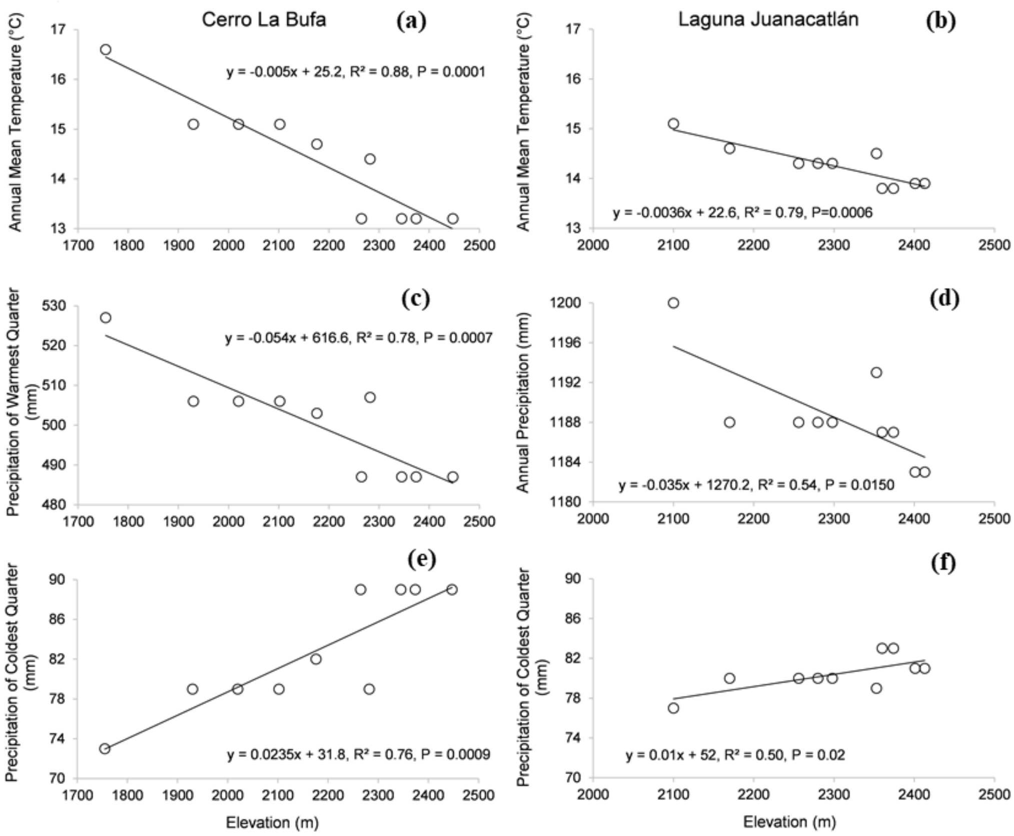


Figure 7. Trends in annual mean temperature BIO 1 (a, b), precipitation of warmest quarter BIO 18 (c), annual precipitation BIO 12 (d), and precipitation of coldest quarter BIO 19 (e, f) in relation to elevation. Cerro La Bufa (B) and Laguna Juanacatlan (J).

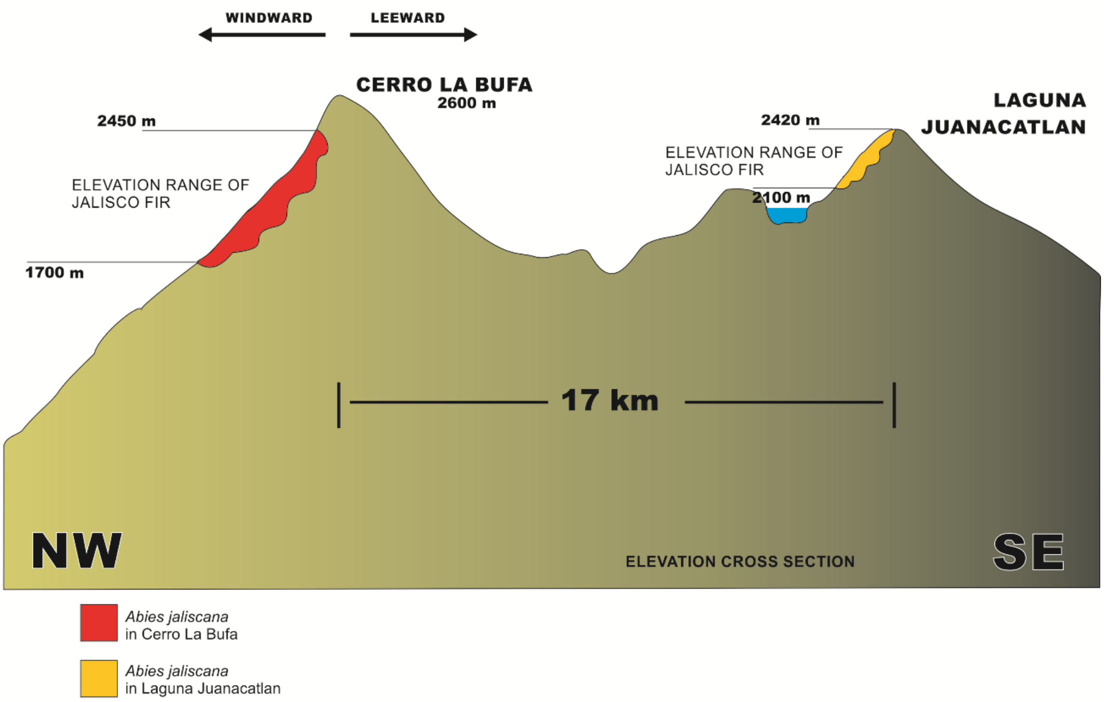


Figure 8. Elevational distribution of the two localities with western Mexican fir forest, which they are oriented towards the windward and are separated by 17 km.

In Mexican fir forests some authors have found a J-inverse shaped size distribution (Encina-Domínguez et al., 2008; Cuevas-Guzmán et al., 2011), suggesting a good regenerative capacity of populations and a regime of mild disturbance, because *Abies* seedlings are generally favored by some canopy openings, a condition which facilitates their establishment and growth (Lara-González, Sánchez-Velásquez & Corral-Aguirre, 2009). The lower belt stands in Laguna Juanacatlan also showed high recruitment but low survival, suggesting some degree of competition with species characteristic of cloud forest, whereas in the upper belt there was a high survival in the categories with the largest trees even in the canopy trees, which were twice abundant than the lower belt. On the other hand, Dang et al. (2010) found a bell-shaped size distribution along an elevational gradient in the Qinling Mountains of China, attributing this pattern to a recruitment pulse due to a period of logging during the 19th century. In contrast, at Cerro La Bufa the lower belt had the highest concentration of individuals in the canopy layer, whereas the middle and upper belts showed a J-inverse pattern. The absence of fir saplings and low recruitment at the lower belt might be attributed to the high competition with high-size heliophilous shrub species in the understory and to the shade of canopy broad-leaved trees. Most of the Mexican fir forests develop in pure stands (Rzedowski, 1978), but *A. jaliscana* shares its distribution in the lower elevation level with several broad-leaved trees and as it reaches a higher elevation, it becomes a nearly monospecific community.

Some authors have stated that boreal forest spreads through the cordilleras of western North America to southern Mexico, and that most of the Mexican highlands are covered by boreal forest (e.g. *Picea* and *Abies*) (Leopold, 1950; Lomolino, Riddle, Whittaker & Brown, 2010). However, this assertion is questioned because the upper limit of annual mean temperature for the boreal forest is around 2 to 3 °C, which is closer to that reported for temperate subalpine forest (e.g. spruce-fir forest in the mountains of eastern North America) (Cogbill & White, 1991). On the other hand, alpine and subalpine belts in the tropics and subtropics have a temperature range close to the boreal forests or subarctic-subalpine needle-leaved forests (3–6 °C) (Holdridge, 1947; Whittaker, 1975; Wolfe, 1979). In contrast, the Mexican "boreal forests", mainly composed by *Abies religiosa* populations (Section *Oiamel*), have an annual mean temperature of 9–10 °C at their upper limit of elevational distribution (Sánchez-Velásquez et al., 1991; Sánchez-González & López-Mata, 2003). These forests can be more accurately referred to as cool-temperate forest than "boreal forest". Furthermore, in the present study we observed that *A. jaliscana* forests are warm temperate moist forests (annual mean temperature: 12–18 °C, see (Holdridge, 1947)), rather than "boreal", in a subtropical montane zone, and they form nearly monospecific forests in areas with 14.5 to 13.8 °C of annual mean temperature and 1215 to 1183 mm of annual precipitation. Therefore, according to climate and the biome concept, Mexican fir forests have more affinity with the "temperate rain forest" biome (TRF-biome) (Whittaker, 1975; Lomolino et al., 2010) than with the boreal forest. In the current study, the genera *Cleyera*, *Magnolia*, and others like *Symplocos* and *Ternstroemia*, are also found in the downward transition to the upper montane cloud forest. Some examples of the former are the mixed broad-leaved evergreen and coniferous forests of southeastern and eastern Asia (e.g. *Abies firma*, *Cleyera japonica*, *Fagus japonica* and *Magnolia hypoleuca*) (Takahashi and Okuhara, 2012). Similar temperature and precipitation parameters in our study area have also been documented in the Redwood forest in western North America, with populations of *Abies grandis* (Table 5) (Noss, 2000), a forest distributed in the warm-temperate and cool-temperate regions. Floristically, they share broadleaved evergreen and deciduous genera such as *Alnus*, *Arbutus*, *Cornus*, *Fraxinus*, *Garrya* and *Quercus*. The climate of the TRF-biome in North America is cool and maritime, with abundant winter rainfall (Temperate and Mediterranean macrobioclimates) (Rivas-Martínez, Rivas-Sáenz & Penas, 2011) and considerable summer cloudiness (little rain) and fog (Whittaker, 1975). These two last attributes coincide partly with the *A. jaliscana* forest, which exhibits little rainfall in winter, high

Table 5. Annual mean temperature (AMT) and annual precipitation (AP) in forests with *Abies* and other conifers.

| Location | Latitude | Elevation (m a.s.l.) | AMT (°C) | AP (mm) | Species/ Genus |
|---|---|---|---|---|---|
| Sierra de Grazalema Natural Park, Spain | 36° | 900−1400 | 15 | 2000 | *Abies pinsapo* |
| Sierra of Zapaliname, Mexico | 25° | 2668−3025 | 12−13 | 560−600 | *Abies vejarii* |
| Sierra Nevada, Mexico | 19° | 3100−3500 | 10−12 | 900−1000 | *Abies religiosa* |
| South-Central B. C., Canada | 51° | 1890−1950 | 1 | >1000 | *Abies lasiocarpa* |
| Bull Creek, California, USA | 41° | 31 | 14 | 1460 | *Abies grandis* |
| Headwaters Forest Reserve, California, USA | 40° | 482 | 10.3 | 1671 | *Abies grandis* |
| Humboldt County, California, USA | 40°−41° | − | 15.9−15.0 | 1222−1679 | *Abies grandis* |
| Qinling Mountains, China | 33° | 2300−2800 | 1−6 | 950−1200 | *Abies fargesii* |
| Eastern Asia | − | − | 10−13 | − | *Abies* and *Tsuga* |
| Upper belt Western Jalisco, Mexico* | 20° | 2300−2413 | 13.2−14.5 | 1183−1217 | *Abies jaliscana* |
| Hokkaido, northern Japan | 43° | − | 5.2−0.7 | 769−1298 | *Abies sachalinensis* |
| Mount Shizumo, central Japan | 35° | 400−500 | 12.6 | 1813 | *Abies firma* |

See references (Wolfe, 1979; Arista, 1995; Noss, 2000; Pelt and Franklin, 2000; Antos and Parish, 2002; Sánchez-González & López-Mata, 2003; Encina-Domínguez et al., 2008; Dang et al., 2010; Takahashi, 2010; Takahashi and Okuhara, 2012; Berrill, Beal, LaFever & Dagley, 2013). (*) This study, data were obtained at WorldClim based on coordinates of this study

fog incidence throughout the year, although the highest rainfall occurs in summer and autumn by the influence of tropical macrobioclimate. Nevertheless, in our study area there is an increase in precipitation of the coldest quarter of the year and fir basal area in relation to elevation. This slight increase in winter rainfall suggests more condensation of moist air at higher elevations compared to lower sites, thus favoring the growth of fir trees. The seasonality is different between TRF of Northwestern North America and the western Mexican fir forests; for the North American TRF the entrance of fog occurs in summer (dry period) (Dawson, 1998), whereas in *A. jaliscana* forests, the fog incidence occurs during the winter-spring period (dry). In both forest biomes this phenomenon is due to their proximity to the ocean. The mix of angiosperms and gymnosperms in the canopy layer is also characteristic of other temperate forests highly influenced by the oceanic moisture, e.g. in New Zealand, Tasmania and southern Chile, which have been described as Oceanic Temperate Forests (OTF) by McGlone, Buitenwerf & Richardson (2016), but these forests, due to their higher latitude, lack a marked dry season (precipitation of the driest month exceeds 35 mm). In contrast, the *A. jaliscana* forests of western Mexico exhibit a precipitation of the driest month less than 7 mm (WorldClim database). The precipitation of the warmest quarter and precipitation of the coldest quarter of the year are very important variables, because provide information about the annual wet-dry threshold and fir forests are mesic, therefore need humidity throughout the year. In summary, due to such climatic and floristic affinities with humid temperate forests, including *Abies* in the northern hemisphere and to similar temperature and precipitation parameters, it is plausible naming *Abies jaliscana* forests as temperate-like biome islands within the Subtropical-type bioclimate region.

## Conclusion

In conclusion, the fir forests in Cerro La Bufa and Laguna Juanacatlan, as in the rest of Mexican fir forests of the TMVB, are linked to warm-cool temperate belts, similar to the observed in other forests like those dominated by *Abies firma* in central Japan or the North American temperate rain forest biome, dominated by *Abies grandis* (in the same Sect. *Grandis*, such as *A. jaliscana*). Our study suggests that the elevation increase (above 2000 m), winter rainfall, persistent moisture throughout the year, annual precipitation above 1100 mm and low mean temperatures (14.5–13.8 °C) in subtropical latitudes, enable a suitable habitat for Jaliscan fir forests; however, other environmental factors such as dispersal, competition and human impact might also play an important role.

Finally, the fir forest in Laguna Juanacatlan seems to be in a healthy condition of conservation, and the forest should be able to maintain itself if not severely disturbed by humans. Global climate change and anthropogenic disturbances such as logging and grazing, could contribute to reduce the extension of Mexican fir forests given that the upward migration of their populations, especially *A. jaliscana*, would not be possible since they grow almost in the mountain summits. The relationship between winter precipitation and dominance of *A. jaliscana* represents a high climatic fragility, because under climate change scenarios it is predicted a decrease in winter precipitation and increases in temperature, which negatively affects early wood and late growth in *A. religiosa* and *Pinus hartwegii* in central Mexico (Astudillo-Sánchez, Villanueva-Díaz, Endara-Agramont, Nava-Bernal & Gómez-Albores, 2017; Carlón-Allende, Villanueva-Díaz, Mendoza & Pérez-Salicrup, 2018). Therefore, we recommend protecting and conserving the *A. jaliscana* forests until new research is carried out; which should include more environmental variables and address relationships between climate and growth estimators, such as dendrochronological studies.

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**Appendix.** List of families and species of woody plants in ten study sites at Cerro La Bufa (B) and ten at Laguna Juanacatlán (J) in western Jalisco, Mexico. Numbers in species rows are species abundance in each site. Site code number is as in Table 1.

| | **Site code** | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Taxa** | **B1** | **B2** | **B3** | **B4** | **B5** | **B6** | **B7** | **B8** | **B9** | **B10** | **J1** | **J2** | **J3** | **J4** | **J5** | **J6** | **J7** | **J8** | **J9** | **J10** |
| **Pinidae** | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| **Cupressaceae** | | | | | | | | | | | | | | | | | | | | |
| *Cupressus lusitanica* | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Pinaceae** | | | | | | | | | | | | | | | | | | | | |
| *Abies jaliscana* | 4 | 9 | 8 | 4 | 1 | 14 | 53 | 28 | 57 | 13 | 35 | 8 | 49 | 50 | 59 | 14 | 16 | 53 | 47 | 52 |
| *Pinus devoniana* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| *Pinus douglasiana* | 1 | - | - | - | - | 1 | - | - | - | - | - | 1 | 2 | 2 | 3 | - | - | - | - | - |
| *Pinus leiophylla* | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 10 | - |
| *Pinus lumholtzii* | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | - | - | - | - | - | - |
| *Pinus montezumae* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 |
| *Pinus oocarpa* | - | - | - | 4 | - | - | - | - | - | - | 3 | - | 2 | - | - | - | - | - | - | - |
| *Pinus pseudostrobus* | - | - | - | - | - | - | 2 | - | - | 2 | 4 | - | - | - | - | - | 1 | - | 1 | - |
| | | | | | | | | | | | | | | | | | | | | |
| **Magnolids** | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| **Lauraceae** | | | | | | | | | | | | | | | | | | | | |
| *Persea hintonii* | - | - | - | - | 4 | - | - | - | - | - | 2 | - | - | - | - | - | - | - | - | - |
| **Magnoliaceae** | | | | | | | | | | | | | | | | | | | | |
| *Magnolia pacifica* | 8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | | | | | | | | | | | | | | | | | | | |
| **Eudicots** | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| **Anacardiaceae** | | | | | | | | | | | | | | | | | | | | |
| *Toxicodendron radicans* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - |
| **Araliaceae** | | | | | | | | | | | | | | | | | | | | |
| *Oreopanax xalapensis* | - | - | 1 | - | 1 | - | 1 | - | - | - | - | 8 | 3 | 3 | - | 1 | 1 | - | - | - |

***Appendix** (continued)*

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Asteraceae** | | | | | | | | | | | | | | | | | | | | |
| *Ageratina areolaris* | 3 | 3 | 1 | - | - | - | - | - | - | - | - | - | 1 | 2 | - | - | - | - | - | - |
| *Baccharis salicifolia* | - | - | - | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Roldana angulifolia* | 20 | 8 | 5 | 1 | 1 | - | - | 7 | 14 | 20 | - | - | - | - | - | - | - | - | - | - |
| *Rumfordia floribunda* | 6 | 4 | 1 | 4 | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - |
| *Telanthophora jaliscana* | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | 6 | - | - | 22 |
| *Verbesina fastigiata* | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Aquifoliaceae** | | | | | | | | | | | | | | | | | | | | |
| *Ilex brandegeana* | - | - | - | - | - | - | - | - | - | - | 3 | - | - | - | - | - | 1 | - | - | - |
| *Ilex dugesii* | - | - | 2 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - |
| *Ilex tolucana* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| **Berberidaceae** | | | | | | | | | | | | | | | | | | | | |
| *Berberis hemsleyi* | - | 3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Betulaceae** | | | | | | | | | | | | | | | | | | | | |
| *Carpinus caroliniana* | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Ostrya virginiana* | 1 | 2 | 1 | 5 | 6 | 3 | - | 33 | - | - | - | - | - | - | - | - | 14 | - | - | - |
| **Celastraceae** | | | | | | | | | | | | | | | | | | | | |
| **Clethraceae** | | | | | | | | | | | | | | | | | | | | |
| *Clethra fragans* | 6 | 3 | 6 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Clethra hartwegii* | - | - | - | - | 19 | 20 | - | 6 | 1 | - | 18 | 26 | 1 | 9 | - | 42 | 14 | - | - | - |
| **Clusiaceae** | | | | | | | | | | | | | | | | | | | | |
| **Cornaceae** | | | | | | | | | | | | | | | | | | | | |
| *Cornus disciflora* | - | - | - | - | - | - | 1 | 2 | - | - | 31 | - | 5 | 2 | - | - | - | - | - | |
| *Cornus excelsa* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | |
| **Ericaceae** | | | | | | | | | | | | | | | | | | | | |
| *Arbutus tesellata* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - |
| *Arbutus xalapensis* | - | - | 2 | 2 | - | 1 | - | - | 3 | 4 | 2 | 4 | 5 | 2 | 14 | 1 | 1 | 2 | 1 | - |
| **Euphorbiaceae** | | | | | | | | | | | | | | | | | | | | |
| *Euphorbia schlechtendalii* | - | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Fabaceae** | | | | | | | | | | | | | | | | | | | | |

***Appendix****(continued)*

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calliandra laevis* | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Inga hintonii* | 8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Fagaceae** | | | | | | | | | | | | | | | | | | | | |
| *Quercus calophylla* | - | 1 | 4 | 2 | - | - | - | - | - | - | 2 | 1 | - | - | - | - | - | 1 | - | 3 |
| *Quercus castanea* | - | - | - | 5 | - | - | - | - | - | - | 3 | - | 2 | 7 | 5 | - | 1 | 4 | 1 | 5 |
| *Quercus crassifolia* | - | - | - | - | - | - | 1 | - | 3 | - | - | - | - | - | - | - | - | - | - | - |
| *Quercus centenaria* | 17 | 9 | 30 | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Quercus laurina* | - | - | - | - | - | - | - | - | - | 3 | - | - | - | - | - | - | - | - | - | - |
| *Quercus martinezii* | - | - | - | 4 | 16 | 4 | - | - | 15 | - | - | - | - | - | - | - | - | - | - | - |
| *Quercus nixoniana* | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - |
| *Quercus obtusata* | - | - | - | 7 | 2 | - | 2 | - | 12 | 1 | 5 | 9 | 4 | 8 | 12 | 2 | - | 3 | 13 | 4 |
| *Quercus rugosa* | - | - | 1 | 1 | - | 1 | - | - | 15 | 2 | - | - | - | - | - | - | - | - | - | - |
| *Quercus scytophylla* | - | - | - | - | - | 1 | - | 11 | - | 3 | - | - | - | 1 | - | - | - | - | - | 1 |
| **Garryaceae** | | | | | | | | | | | | | | | | | | | | |
| *Garrya longifolia* | - | - | - | - | - | - | 9 | - | 13 | - | - | 3 | 3 | - | - | 1 | - | - | 1 | - |
| **Melastomataceae** | | | | | | | | | | | | | | | | | | | | |
| *Conostegia volcanalis* | 6 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Miconia albicans* | - | 1 | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Myrtaceae** | | | | | | | | | | | | | | | | | | | | |
| *Eugenia culminicola* | - | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Eugenia sp.* | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Oleaceae** | | | | | | | | | | | | | | | | | | | | |
| *Fraxinus uhdei* | - | - | - | - | - | - | 22 | - | - | - | - | - | - | - | - | - | - | - | 1 | - |
| **Pentaphylacaceae** | | | | | | | | | | | | | | | | | | | | |
| *Cleyera integrifolia* | - | 1 | - | - | - | - | - | - | - | - | 10 | 3 | 1 | 9 | 3 | 1 | 8 | - | - | - |
| *Symplococarpon purpusii* | 8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Ternstroemia lineata* | 3 | 3 | 2 | - | - | - | - | 1 | 32 | 17 | - | - | 21 | 1 | - | 2 | 27 | - | - | - |
| **Primulaceae** | | | | | | | | | | | | | | | | | | | | |
| *Myrsine juergensenii* | - | - | - | - | - | - | - | - | - | - | 5 | 1 | 8 | 13 | - | - | 1 | - | - | - |
| **Rosaceae** | | | | | | | | | | | | | | | | | | | | |

***Appendix****(continued)*

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crataegus mexicana* | - | - | - | - | - | - | 2 | - | - | - | - | 2 | - | - | 13 | - | - | 2 | - | 3 |
| *Prunus cortapico* | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Prunus serotina* subsp. *capuli* | - | - | - | - | - | - | 3 | - | - | - | 2 | - | - | 1 | 1 | - | - | - | - | 1 |
| **Rubiaceae** | | | | | | | | | | | | | | | | | | | | |
| *Glossostipula concinna* | - | - | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Sabiaceae** | | | | | | | | | | | | | | | | | | | | |
| *Meliosma dentata* | - | - | - | - | 2 | - | - | - | - | 2 | 1 | 38 | - | 1 | - | 1 | 3 | - | - | - |
| **Styracaceae** | | | | | | | | | | | | | | | | | | | | |
| *Styrax argenteus* | - | - | - | - | - | - | - | - | - | - | 50 | 20 | 48 | 114 | 33 | 47 | 18 | 14 | 30 | 20 |
| *Styrax radians* | 24 | 12 | 20 | 14 | 6 | 8 | - | 17 | - | 4 | - | - | - | - | - | - | - | - | - | - |
| **Symplocaceae** | | | | | | | | | | | | | | | | | | | | |
| *Symplocos citrea* | - | - | - | - | - | - | - | - | - | - | 3 | 19 | 2 | 18 | 3 | 9 | 33 | 1 | - | - |
| **Verbenaceae** | | | | | | | | | | | | | | | | | | | | |
| *Lippia umbellata* | - | - | - | - | - | - | - | - | - | 3 | - | - | - | - | - | - | - | - | - | - |
| **Vitaceae** | | | | | | | | | | | | | | | | | | | | |
| *Vitis sp.* | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| **Salicaceae** | | | | | | | | | | | | | | | | | | | | |
| *Xylosma flexuosa* | 8 | 14 | 2 | - | - | - | 6 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Morphospecies 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Morphospecies 2 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |