Relationship between vegetation structure and microenvironment in *Fagus grandifolia* subsp. *mexicana* forest relicts in Mexico

Ernesto Ch. Rodríguez-Ramírez¹, Arturo Sánchez-González²,* and Gregorio Ángeles-Pérez³

¹ Laboratorio de Biogeografía y Sistemática, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México
² Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Ciudad Universitaria; Carretera Pachuca-Tulancingo Km. 4.5, Mineral de la Reforma 42184, Hidalgo
³ Postgrado en Ciencias Forestales, Colegio de Postgraduados, Montecillo 56230, Texcoco, Estado de México, México
* Correspondence address. Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Ciudad Universitaria; Carretera Pachuca-Tulancingo Km. 4.5, Mineral de la Reforma 42184, Hidalgo. Tel: 017717172000 ext 6676; Fax: 0177171722112; E-mail: arturosg@uaeh.edu.mx

Abstract

**Aims**
Changes in the structure and composition of forests, whether caused by natural or anthropic events, alter the microenvironment, sometimes irreversibly. Since the local environment has a direct impact on basic ecological processes, this has become a key component of research. Mexican beech forests (*Fagus grandifolia* subsp. *mexicana*) in the Sierra Madre Oriental are restricted to sites with specific climate, soils and topography, making them an ideal natural system for ecological research. The objectives of this study were to identify the relationship between the microenvironment and the tree and shrub structure and composition of Mexican beech forests in the state of Hidalgo, and to compare the floristic similarity of these forests on the country scale using data from seven localities.

**Methods**
Specimens were collected for a period of one year at all localities in the state of Hidalgo where beech forests are located. At each locality, five 400 m² plots were established, and structural attributes (basal area, coverage, density and species richness) and six environmental variables were measured in the plots. The relationship between structure and microenvironment was estimated by simple correlation and canonical correspondence analysis (CCA). In addition, floristic similarity between different beech forest localities in the Sierra Madre Oriental was estimated by correspondence analysis (CA).

**Important Findings**
Twenty tree species and eight shrub species were identified; at all localities studied *F. grandifolia* subsp. *mexicana* dominated the canopy. The multivariate analysis indicated that (i) in the four localities in the state of Hidalgo, all microenvironmental variables except pH are related to the variation observed in species composition and structure; (ii) the El Gosco locality had both tree and shrub species and microenvironmental factors different from those observed in the *Fagus* forests at the other localities in the study and (iii) the localities studied in order to draw country-scale comparisons could be divided into three groups by floristic similarity. The first group consisted of the Hidalgo localities, the second of the Veracruz localities, and the third, more different from the others, of the Tamaulipas locality. The results of this study provide the first reference for the relationship between the range of microenvironments and species structure in Mexican beech forests. Microenvironmental conditions in the larger beech forests could be used as a model for designing management and conservation programs for this plant association. Because of its particular ecological and historical characteristics, this association could serve as an example of biodiversity conservation in Mexico.

**Keywords:** Canonical correspondence analysis, *fagus* forest, floristic composition, *Mexico*, montane cloud forest, richness

Received: 2 June 2015, Revised: 2 December 2016, Accepted: 10 December 2016
INTRODUCTION

In terrestrial ecosystems, the microenvironment plays a decisive role in the germination, growth, reproduction and mortality of plant species, since it has a direct and indirect influence on fundamental processes such as photosynthesis, evapotranspiration and nutrient cycles (Behera et al. 2012; Godfroid et al. 2006; Xu et al. 2004). Changes in vegetation structure and composition caused by human activities (habitat fragmentation through conversion to agricultural uses, climate change and illegal logging) as well as natural disturbances (tree fall, fires, droughts, hurricanes, insects and disease, windstorms) alter local conditions (Chen et al. 1999; Gehlhausen et al. 2000).

Microenvironment is the result of the interaction of multiple biotic and abiotic factors. Thus, any change in the micro-environment has effects, sometimes drastic, on structural and ecosystem processes and vice versa (Behera et al. 2012). Among widely documented microenvironmental changes in forest ecosystems are: increased levels of solar radiation, air and soil temperature, and wind speed; and decreases in vapor pressure, relative humidity and soil moisture, and the amount of leaf litter (Beckage and Clark 2003; Chen et al. 1999; Gehlhausen et al. 2000).

The montane cloud forest (MCF) provides an interesting system for analyzing the relationship between microenvironment and changes in vegetation structure and composition due to its high degree of fragmentation in tropical mountains around the world and because this forest requires specific environmental conditions (Ponce-Reyes et al. 2012). A further reason for interest in these systems is that they are among the richest terrestrial ecosystems in terms of number of plant species per unit area, and at the same time, one of the most fragile and vulnerable (Ledo et al. 2009). In Mexico, less than 1% of the country’s land area is MCF. It is distributed along the main mountain ranges in an elevation range of 1000 to 2500 m (Villasenor 2010). It thrives at sites with heterogeneous geographical and ecological characteristics, with steep slopes and windward slopes where soil moisture and atmospheric humidity are high most of the year (González-Espinosa et al. 2011). The MCF is currently under serious threat due mainly to climate change, changes in land use, and high rates of deforestation (Cruz-Cárdenas et al. 2012; Ponce-Reyes et al. 2012).

In the Mexican MCF a type of plant association grows that is known as Fagus or beech forest. Its canopy is dominated by Fagus grandifolia subsp. mexicana (Martínez) E. Murray, a taxon listed as rare, vulnerable and endangered in the International Union for Conservation of Nature and Natural Resources (IUCN) Red List and included in the Official Mexican Standard NOM-059 in the category of endemic and endangered species (SEMARNAT 2010). Mexican beech forests are relicts that were cut off from beech forests in Eastern Canada and the United States in the Pleistocene. Since then, they have continued to grow under unique environmental conditions, isolated from their northern counterparts (Fang and Lechowicz 2006; Montiel-Oscura 2011).

Currently, the total area of Mexican beech forest is ~144.54 hectares, distributed in isolated fragments in the mountains of the Sierra Madre Oriental range at elevations of 1400 to 2000 m in the states of Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, Puebla and Veracruz (Montiel-Oscura et al. 2013; Rodríguez-Ramírez et al. 2013; Rowden et al. 2004). The high degree of habitat disturbance is rapidly decreasing the size and number of these forests (Ortiz-Quijano et al. 2015; Rodríguez-Ramírez et al. 2013; Rowden et al. 2004). In addition, it is estimated that the number of these forests will shrink drastically in the near future as a consequence of global warming (Téllez-Valdés et al. 2006).

Quantifying variation in microenvironmental conditions may help explain spatial and temporal changes in species composition and the structure and function of ecosystems, enabling a better understanding of their dynamics (Bunyan et al. 2012; Chen et al. 1999; Nunes and Maës 2006). The ecological requirements of Fagus sp. forests in cold temperate climates in Asia, Canada, the United States and Europe are relatively well known. In contrast, information on beech forests in subtropical or warm temperate climates is scarce. These forests are found only in Taiwan, China (F. hayatae) and in Mexico (Peters 1997; Pignatti et al. 2006).

The present study was undertaken in view of the current restricted distribution of beech forest in Mexico, its high degree of fragmentation, the limited data on its structure and composition, and the fact that climate, topography, soil and exposure conditions are highly specific in places where it grows (Fang and Lechowicz 2006; Peters 1997; Rodríguez-Ramírez et al. 2013). The objectives of the study were: (i) to determine the composition and structure of Fagus forests, based on relative importance values (RIVs) of the tree and shrub species present; (ii) to estimate the relationship between microenvironmental factors, species composition and vegetation structure and (ii) to analyze floristic similarity (or beta diversity) between different localities with Fagus forest of Mexico, based on the RIV of tree and shrub species.

MATERIAL AND METHODS

Study area

Fagus forests are distributed in the Sierra Madre Oriental, a physiographic unit over 800 km long and 80–100 km wide (Eguiluz de Antuñano et al. 2000). It is bounded by the Texas Platform to the north, the Rhyolitic Central Plateau to the west and southeast, the Transmexican Volcanic Belt to the south and the Gulf of Mexico Cenozoic Coastal Plain to the east. Due to its irregular topography, the MCF contains favorable ecological conditions for the growth of Fagus forest in certain places, such as streams and ecotonal areas between conifer and Quercus forests (Peters 1997).
The climate most characteristic of Fagus forest in Mexico is humid temperate, C (fm), the precipitation and mist regime is constant throughout the year, but there are a season of lower humidity, with <60 mm rainfall per month, between November to April. Total annual precipitation ranges from 1200 to 2050 mm and mean annual temperature from 12.7 to 14°C (García 1988; Gual-Díaz and Rendón-Correa 2014; Peters 1997).

The study area included all localities where Fagus forest is found in the state of Hidalgo (A–D, Fig. 1). Plant composition, vegetation structure, species richness and microenvironment were analyzed throughout the entire study area. Detailed information on the coverage, degree of fragmentation and environmental history of each individual forest can be found in the studies by Rodríguez-Ramírez et al. (2013) and Ortiz-Quijano et al. (2015, 2016). For the analysis of similarity among Mexican beech forests, the study areas were the four localities listed above (A–D) and three further localities (E–G) previously studied by Williams-Linera et al. (2000, 2003). It should be noted that the Fagus forest in the states of Hidalgo, Tamaulipas and Veracruz has a total land area of ~119 ha, which is 82% of the total known area covered by this plant association in Mexico (Rodríguez-Ramírez et al. 2013).

Floristic composition and vegetation structure
Specimens of vascular plants with tree and shrub life forms were collected quarterly during a period of one year (January to December, 2013) at each locality. An exhaustive search and collection effort was made, covering the entire area of each forest on foot. Collection of specimens was restricted to the edges, so as not to include in the inventory species characteristic of disturbed environments or other plant associations. The species present at each site were identified using specific taxonomic keys for each family. In order to complement data on numbers of species, samples previously collected in Mexican beech forests and stored in the MEXU national herbarium, Institute of Biology, National Autonomous University of Mexico and in the XAL herbarium, Instituto de Ecología A.C. were consulted. The nomenclature of vascular plant species was updated at the Tropicos website (tropicos.org, 2014) of the Missouri Botanical Garden. The specimens collected in this study were deposited in the collection of the HGOM herbarium of the Universidad Autónoma del Estado de Hidalgo. To identify the structural importance of tree and shrub species, at each locality five 20 × 20 m sample plots ~60 m apart were selected. Basal area (BA) was estimated for trees with normal diameter at 1.30 m height (dbh) ≥1.5 cm, coverage (C) for shrubs, and density of individuals of each species for both life forms. BA was calculated using the formula $AB = \pi r^2$, where $r = 3.1416 \times (1/2) (dbh)$ is the tree radius (Matteucci and Colma 1982). Coverage of shrubs (C) is given by the formula

$$
C = \pi \left[ \frac{1}{4} (d_1 + d_2) \right]^2,
$$

where $d_1$ and $d_2$ are the major and minor axis diameters perpendicular to each other in the vertical projection of the shrub canopy. From the relative values of BA, C and density, the RIV of each species (Mueller and Ellenberg 1974) was estimated as follows: RIV = (1/2) (relative BA + relative density) for tree species, and RIV = (1/2) (relative cover + relative density) for shrub species. In addition, semi-realistic profile diagrams were drawn to visually represent the composition and structure of each forest.

Microenvironmental variables
In each sample plot, the following microenvironmental factors were measured: soil moisture, temperature and pH, amount and depth of litter, and canopy cover (Fang and Lechowicz 2006). The data were measured between 9:00 am and 12:00 pm to standardize the daily humidity fluctuation (Barrientos 2012), for a one-year period (January to December 2013) at three-month intervals. For the statistical analysis of the data, the input values used to represent the factors for each sample plot were an average of four measurements taken at the four cardinal points of the plot.

(i) ‘Soil moisture’ was recorded at a depth of 2–3 cm using a hygrometer (Lincoln Soil Moisture Meters). This factor took values on a scale from 1 to 10, where 1 = dry and 10 = saturated.

(ii) ‘Soil temperature’ was measured with a soil thermometer (Taylor® Switchable Digital Pocket Thermometer).

(iii) ‘Quantity of litter’ was measured by collecting wet leaf litter, small branches and fragmented litter material from 50 × 50 cm plots (as an indirect estimate of the quantity

\[ Downloaded from https://academic.oup.com/jpe/article-abstract/11/2/237/2738897 by guest on 15 April 2019 \]
of organic matter: carbon-rich material formed by animal, plant and microbial residue in various stages of decomposition in plastic bags and weighing it on a digital scale. It was then returned to the forest floor at the sampling site.

(iv) ‘Litter depth’ was measured by inserting a ruler into the ground until it touched the mineral soil layer at each of the four cardinal points of the sample plot.

(v) ‘Soil pH’ was estimated by taking a sample of soil from a depth of ~10 cm. The sample was placed in sealed bags, which were labeled with the information of the respective site. Later in the laboratory four measurements were taken of each sample using a potentiometer (reference buffer pH 7.00 ± 0.01 at 25°C).

(vi) ‘Canopy cover’ was estimated in each sample plot using a concave mirror forestry densitometer (Forestry Suppliers Spherical Crown Densiometers, model A).

Relationship between microenvironment and species richness

Analysis of variance tests and Tukey multiple comparisons of means were used to assess whether the values of the microenvironmental factors differed significantly between study sites (Zar 1999). Both analyses were carried out using the SigmaStat program version 3.5 (Jandel Scientific 2006). Additionally, the Pearson correlation coefficient between the microenvironmental factors (moisture and soil temperature, quantity and depth of litter, pH and canopy cover) and tree and shrub species richness (average number of species in five 400 m² plots per locality) was calculated using the Statistica program v.7 (StatSoft, Inc. 2004). In order to compare total species richness between different sized localities, the taxonomic biodiversity index (BI) was used. The index is calculated by dividing the number of species recorded (S) by the natural logarithm of area (A) in hectares; IB = S/ln A (Squeo et al. 1998).

Species composition, vegetation structure and microenvironment

To estimate the relationship between species composition and vegetation structure with respect to local variation in microenvironmental conditions at four Fagus forest localities (El Gosco, La Mojonera, Medio Monte and Tutotepec), a canonical correspondence analysis was carried out on data matrices of the species RIV and the mean values of the four measurements of each factor, by sample plot. The CANOCO program v.4.5 (Ter Braak and Šmilauer 2002) was used for this analysis.

Floristic similarity among Mexican beech forests

To determine similarity in species composition and structure of Mexican beech forests, a correspondence analysis (CA) was carried out on the RIV data and the data on tree and shrub species obtained in the present study (Localities A–D, state of Hidalgo) and the sites in the states of Veracruz and Tamaulipas (Localities E–G, Williams-Linera et al. 2000, 2003). The CA was carried out using the CANOCO v. 4.5 program (Ter Braak and Šmilauer 2002).

RESULTS

Floristic composition and vegetation structure

In all, 20 tree species and eight shrub species were identified (Table 1). At the La Mojonera and Medio Monte localities the same numbers of species were recorded: 15 tree and 4 shrub species. Of these, 10 of the tree species and two of the shrub species were present at both sites. At the El Gosco locality, 13 tree and 7 shrub species were found, and at Tutotepec, 11 tree and 3 shrub species. However, when the values of species richness are taken per unit area, the picture is different: in this case the El Gosco locality, with a BI of 13.3, showed more than double the number of species than the other three localities in Hidalgo (Table 1).

The tree species with the highest RIV at all four localities was F. grandifolia subsp. mexicana, followed by Magnolia schiedeana for Medio Monte and Tutotepec, Quercus delgadoana for La Mojonera and Pinus patula for El Gosco (Table 1). The Fagus individuals with the largest diameters were observed at La Mojonera (dbh ≥ 100 cm). At El Gosco, Medio Monte and Tutotepec, the largest tree diameters ranged between 88 and 90 cm.

Tree species commonly found in all the localities studied were Clethra mexicana, M. schiedeana and Quercus spp., and Miconia glaberrima in the shrub layer. The tree ferns Cyathea fulva and Dicksonia sellowiana proved to be important structural elements at the La Mojonera, San Bartolo and Tutotepec localities due to their high density of individuals (Table 1).

In terms of density, Fagus accounts for 66% of individuals of all tree species at Tutotepec, 62.7% at La Mojonera, 51% at Medio Monte and 39% at El Gosco. The semi-realistic profiles enable the differences in species composition and Fagus forest structures between locations to be visualized (Fig. 2).

Relationship between species richness and microenvironment

The values of some of the microenvironmental factors differed significantly between localities; the most divergent results were at the El Gosco locality with low values of litter quantity and depth, and high values of soil temperature (P < 0.05), and La Mojonera, where pH values, tree cover, soil moisture and temperature differ significantly (P < 0.05) from those at the other locations. In contrast, the values of the microenvironmental variables were similar for the Medio Monte and Tutotepec localities, and the only significant difference (P < 0.05) between the two was for litter depth (Fig. 3).

According to the results, species richness of trees and shrubs at the localities analyzed correlated significantly only with soil pH (r = −0.26); the amount of litter with soil moisture (r = 0.41); and soil temperature with litter depth (r = −0.38) and soil moisture (r = −0.28). Correlations between tree cover
### Table 1: Plant species composition (trees and shrubs) of the Mexican beech forests

<table>
<thead>
<tr>
<th>Trees</th>
<th>Mexican beech forests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
</tr>
<tr>
<td>Fagus grandifolia subsp. mexicana (Martínez) A.E. Murray</td>
<td>48.14</td>
</tr>
<tr>
<td>Magnolia schiedeana Schltdl.</td>
<td>11.96</td>
</tr>
<tr>
<td>Quercus laurina (Liebm.) Wenz.</td>
<td>1.67</td>
</tr>
<tr>
<td>Symphoricarpos limoncillo Bonpl.</td>
<td>0.94</td>
</tr>
<tr>
<td>Ostrya virginiana (Mill.) K. Koch</td>
<td>0.27</td>
</tr>
<tr>
<td>Podocarpus reichel J. Buchholz &amp; N.E. Gray</td>
<td>1.10</td>
</tr>
<tr>
<td>Quercus eugeniifolia Liebm.</td>
<td>1.51</td>
</tr>
<tr>
<td>Eugenia capulí (Schltdl. &amp; Cham.) Hook. &amp; Arn.</td>
<td>1.22</td>
</tr>
<tr>
<td>Clethra mexicana DC.</td>
<td>2.40</td>
</tr>
<tr>
<td>Quercus delgadoana S. Valencia, Nixon &amp; L. M. Kelly</td>
<td>19.49</td>
</tr>
<tr>
<td>Pinus patula Schltdl. &amp; Cham.</td>
<td>2.32</td>
</tr>
<tr>
<td>Quercus trinitatis Trel.</td>
<td>2.81</td>
</tr>
<tr>
<td>Quercus germana Schltdl. &amp; Cham.</td>
<td>1.16</td>
</tr>
<tr>
<td>Quercus xalapensis Bonpl.</td>
<td>0.94</td>
</tr>
<tr>
<td>Cyathea fulva (M. Martens &amp; Galeotti) Fée</td>
<td>0.12</td>
</tr>
<tr>
<td>Dicksonia sellowiana Hook.</td>
<td>—</td>
</tr>
<tr>
<td>Liquidambar styraciflua L.</td>
<td>—</td>
</tr>
<tr>
<td>Prunus serotina Ehrh.</td>
<td>—</td>
</tr>
<tr>
<td>Cleyera theaësides (Sw.) Choisy</td>
<td>—</td>
</tr>
<tr>
<td>Ternstroemia sylvatica Schltdl. &amp; Cham.</td>
<td>—</td>
</tr>
<tr>
<td>Vaccinium leucanthum Schltdl.</td>
<td>—</td>
</tr>
<tr>
<td>Oreocephalus xalapensis (Kunth) Decne. &amp; Planch.</td>
<td>—</td>
</tr>
<tr>
<td>Prunus samyoides Schltdl.</td>
<td>—</td>
</tr>
<tr>
<td>Weinmannia intermedia Schltdl. &amp; Cham.</td>
<td>—</td>
</tr>
<tr>
<td>Drimys granadensis var. mexicana (DC.) A.C. Sm.</td>
<td>—</td>
</tr>
<tr>
<td>Carpinus caroliniana Walter</td>
<td>—</td>
</tr>
<tr>
<td>Chionochloa pachyphylla Wernham</td>
<td>—</td>
</tr>
<tr>
<td>Gymnanthes longipes Müll. Arg.</td>
<td>—</td>
</tr>
<tr>
<td>Ilex discolor Hemsl.</td>
<td>—</td>
</tr>
<tr>
<td>Pinus montezumae Lamb.</td>
<td>—</td>
</tr>
<tr>
<td>Rhamnus caroliniana Blanco</td>
<td>—</td>
</tr>
<tr>
<td>Quercus sartorii Botteri, M. ex A. DC.</td>
<td>—</td>
</tr>
<tr>
<td>Clethra pringlei S. Watson</td>
<td>—</td>
</tr>
<tr>
<td>Shrub and others</td>
<td>—</td>
</tr>
<tr>
<td>Miconia glabrerrima (Schltdl.) Naudin</td>
<td>67.02</td>
</tr>
<tr>
<td>Sambucus nigra L.</td>
<td>12.47</td>
</tr>
<tr>
<td>Nectandra heydiana Mez &amp; Donn. Sm.</td>
<td>1.04</td>
</tr>
<tr>
<td>Epilobium virginianum (L.) W.P.C. Barton</td>
<td>11.80</td>
</tr>
<tr>
<td>Marattia weinmanniiifolia Liebm.</td>
<td>—</td>
</tr>
<tr>
<td>Cornus excelsa Kunth</td>
<td>—</td>
</tr>
<tr>
<td>Tilia americana var. mexicana (Schltdl.) Hardin</td>
<td>—</td>
</tr>
<tr>
<td>Viburnum caudatum Greenm.</td>
<td>—</td>
</tr>
<tr>
<td>Leandra melanodésma (Naudin) Cogn.</td>
<td>—</td>
</tr>
<tr>
<td>Palicourea sp. Aubl.</td>
<td>—</td>
</tr>
<tr>
<td>Gaultheria acuminata Schltdl. &amp; Cham.</td>
<td>—</td>
</tr>
<tr>
<td>Euonymus acuminatus Raf.</td>
<td>—</td>
</tr>
</tbody>
</table>
and the other microenvironmental factors were not statistically significant (in all cases $n = 84$).

### Relationship between composition and vegetation structure and microenvironment

The values of the characteristic roots for the first two ordination axes were $\lambda_1 = 0.431$ and $\lambda_2 = 0.255$; the two axes explained 84.7% of the variation in the data (Table 2). However, the length of the gradient for the first two axes was less than two standard deviations, so the range of variation was small. The scatter plot of species structural values and composition shows that the forest at the El Gosco locality is different from the forests at La Mojonera, Medio Monte and Tutotepec. All the microenvironmental factors analyzed except pH are correlated with the variation in the vegetation structure data: for the first ordination axis, the quantity and depth of litter, canopy cover and soil moisture; for the second axis, soil temperature (Fig. 4, Table 2).

**Table 1: Continued**

<table>
<thead>
<tr>
<th>Trees</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ternstroemia sylvatica</em> Schltdl. &amp; Cham.</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>6.59</td>
<td>8.17</td>
<td>8.23</td>
</tr>
<tr>
<td><em>Citharexylum ligustrinum</em> Van Houtte</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>14.63</td>
<td>—</td>
</tr>
<tr>
<td><em>Cassia floribunda</em> Cav.</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>5.21</td>
</tr>
<tr>
<td>Others</td>
<td>7.67</td>
<td>5.26</td>
<td>12.72</td>
<td>14.21</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total species per site</td>
<td>19</td>
<td>14</td>
<td>19</td>
<td>20</td>
<td>19</td>
<td>19</td>
<td>15</td>
</tr>
<tr>
<td>Area (ha)</td>
<td>42.5</td>
<td>14.0</td>
<td>34.3</td>
<td>4.5</td>
<td>4.0</td>
<td>4.1</td>
<td>4.1</td>
</tr>
<tr>
<td>IB</td>
<td>5.1</td>
<td>5.3</td>
<td>5.4</td>
<td>13.3</td>
<td>17.3</td>
<td>13.7</td>
<td>10.6</td>
</tr>
</tbody>
</table>

The species were ordered with based on the value importance index (IVI). Data from present study (localities in Hidalgo State) and of the work of Williams-Linera et al. (2000, 2003). A = La Mojonera, B = Medio Monte, C = Tutotepec, D = El Gosco, E = “El Cielo” Biosphere Reserve, F = Mesa de la Yerba, G = Acatlan Volcano.
Floristic similarity among Mexican beech forests

The first two axes of the CA ($\lambda_1 = 0.56; \lambda_2 = 0.39$) accounted for 50% of the variation in the data. Three groups defined by similarity in species composition can be observed in the ordination diagram (Fig. 5). The first consists of Fagus forests in the state of Hidalgo (La Mojonera, Medio Monte, Tutotepec and El Gosco), the second of those in the state of Veracruz (Mesa de la Yerba and Volcán Acatlán localities), and the last group, which is more different from the others, is the El Cielo Biosphere Reserve forest, located in the state of Tamaulipas.

**DISCUSSION**

Floristic composition and vegetation structure

Although floristic patterns and ecological processes common to Fagus forests around the world have been documented, a clear trend towards differentiation in the composition of woody plant species and structure in these forests has also been found, which varies according to their geographical location in regions of Asia, Europe and North America where Fagus species are distributed (Hukusima et al. 2013; Peña et al. 2011; Peters 1997). There is also variation in the number and...
identity of tree species coexisting in these forests; the dominance status of *Fagus* varies from being the only tree species to mixed forests where they have a secondary importance in the canopy (Peters 1997; Williams-Linera et al. 2003).

The Mexican beech forests show a unique kind of partner-ship due to their relict status, high degree of isolation, and their vast geographical distance from the more northerly *Fagus* forests that cover large areas of Canada and the United States (Fang and Lechowicz 2006; Denk and Grimm 2009). These characteristics translate into a considerable difference in vascular plant species composition, although similarity is evident at the genus level (Hukusima et al. 2013; Peters 1997). The results of this study are interesting because they indicate that even within a small region (the Sierra Madre Oriental of Mexico) and relatively short distances (less than 10 km linear distance between localities), some appreciable differences attributable to different factors can be detected among the beech forests of Mexico in their tree and shrub species composition and structure.

At all localities analyzed, the species with the most structural importance was *F. grandifolia* subsp. *mexicana*. However, the RIV of this taxon differed between localities; it was generally higher at Medio Monte, La Mojonera and Tutotepec, which can be considered mature forest (Ortiz-Quijano et al. 2016), with a high degree of connectivity, low degree of fragmentation and area greater than 10 ha. In contrast, in the El Gosco beech forest which has high fragmentation, low connectivity and a land area of less than 4.5 ha (Rodríguez-Ramírez et al. 2013), the RIV of *Fagus* was lower and other species showed greater structural significance. Consistent with this, Williams-Linera et al. (2003) note that in some small (less than 4.2 ha) fragments of beech forest in Veracruz, Mexico, the importance of *Fagus* in the canopy varies from being the only tree species, to codominance with mainly *Carpinus caroliniana, Liquidambar styraciflua, M. schiedeana, Pedocarpus sp. and Quercus spp.* At all the localities analyzed by these authors, they found evidence of disturbance; traces of fires, livestock grazing, and harvesting and extraction of firewood. In the specific case of the stand at the Acatlán volcano crater, Williams-Linera et al. (2003) report that it was established after a severe disturbance that destroyed the forest, which explains the exclusive dominance of *Fagus* in the canopy at this site.

Some studies on the local scale in USA and Europe have shown similar results; that is, the structural importance of *F. grandifolia* or *F. sylvatica*, respectively, is lower in forests that have a higher degree of natural and/or anthropogenic disturbance (Peters and Platt 1996; Rozas 2004). Natural or pristine *Fagus* forests in all parts of the world seem to be characterized by the coexistence of several tree species in the canopy (commonly the genus *Quercus*), while unmixed *Fagus* forests are of secondary origin, shaped by human activity and severe natural disturbance in the past (Ballian 2011; Hukusima et al. 2013; Novotný and Frýdl 2011; Peters 1997).

In the beech forests of the state of Hidalgo, similar patterns were observed to those described in the previous paragraph. The species that coexist and dominate the canopies of beech forests differ between localities and the differences are more apparent with greater geographical distance, a larger forest and/or a greater degree of disturbance (Ortiz-Quijano et al. 2016; Rodríguez-Ramírez et al. 2013). For example, some important components of the El Gosco forest are *C. mexicana, L. sylvatica, Persea aff. americana, P. patula* and *Podocarpus reichei*. These are species that can be considered opportunistic, indicators of disturbance and/or of a warmer climate and lower water availability (Jardel-Peláez et al. 2014; Ramírez-Marcial et al. 2001). It is likely that these species thrive and gain structural importance due to the removal of *Quercus* spp. individuals from the canopy, which are an important and common component in mature beech forests (Ortiz-Quijano et al. 2015, 2016); but in Mexico they are also preferred by residents of the villages located near these temperate forests for firewood and charcoal production (González-Espinosa et al. 2011; Ramírez-Marcial et al. 2001).

In contrast, the Medio Monte and Tutotepec localities hold two of the largest fragments of beech forest in Mexico and with the least evidence of disturbance (Ortiz-Quijano et al. 2015; Rodríguez-Ramírez et al. 2013) Here, the structural values of the tree ferns *C. fulva* y *D. sellowiana* were higher than at the other locations analyzed. These results are important.
because the presence of populations of these species of ferns indicates moderate temperature conditions, water availability throughout almost the whole year, and high canopy cover, which are typical of mature MCF (Kessler et al. 2011).

Tree and shrub species richness per unit area was considerably different at El Gosco than at the other three localities. At La Mojonera, Medio Monte and Tutotepec (Fig. 3), where *F. grandifolia* subsp. *mexicana* largely dominates the canopy (mature forests), species richness was lower (between 5.1 and 5.4). At El Gosco, where the beech forest had a higher degree of fragmentation and disturbance, species richness was higher (13.3). It is likely that the dominance of *F. grandifolia* subsp. *mexicana* in terms of coverage and density is promoting or limiting the establishment and growth of other tree and shrub species. The higher values of tree and shrub species richness at the El Gosco locality could be related to recent and increasingly frequent disturbance due to selective and unregulated logging of *Fagus* and *Quercus* trees. The same pattern can be observed on the regional scale: BI values for the beech forests (5.1 to 13.7) are similar to or less than those of other forest associations that make up the MCF in Mexico; for example, BI is 12.6 in Tlanchinol (30,000 ha) and 20.2 in Lolotla (1022 ha), two municipalities in the state of Hidalgo. In both of these municipalities, the MCF (unlike the beech forests) is moderately disturbed and several tree species coexist in the canopy (Luna et al. 1994; Ponce-Vargas et al. 2006). According to the intermediate disturbance hypothesis, gaps created by fallen trees and/or tree removal (a greater disturbance) promote the coexistence of species with different resource use strategies (especially the use of light as a resource). That is, species richness is higher in gaps than under the closed canopy, as has been shown in temperate forests (including *Fagus* spp. forests) in various parts of the world (Grau 2004; von Oheimb et al. 2007; Peña et al. 2011; Peters 1997).

**Relationship between composition, vegetation structure and microenvironment**

The multivariate analysis results show that differences at the state level in species composition and the spectrum of variation in microenvironmental conditions between *Fagus* forest are small but perceptible. These results confirm those reported by other authors, in the sense that the distribution pattern of this plant association is highly restricted within the MCF of Mexico, since it can only thrive in places where the range of variation in environmental conditions (mainly moisture, temperature, topography, exposure and degree of disturbance) is narrow (Fang and Lechowicz 2006; Pignatti et al. 2006; Peters 1997; Rodríguez-Ramírez et al. 2013; Rowden et al. 2004; Williams-Linera et al. 2000, 2003). This has led to suggestions that the survival of *Fagus* forests in the future is uncertain (due to the increase in intensity and frequency of anthropogenic disturbance at the local level and to climate change), and depends largely on the implementation of management programs for their conservation and restoration (Rodríguez-Ramírez et al. 2013; Williams-Linera et al. 2003).

The present study provides the first data on variation in microenvironmental conditions in *Fagus* forests in Mexico. Although the results are at the state level, this plant association is well represented in Hidalgo, since the state contains 73.9% of the total forest of this type in Mexico (Montiel-Oscura 2011; Rodríguez-Ramírez et al. 2013). Characterization of the microenvironment in forest ecosystems is currently considered to be particularly important because its direct influence on key ecological processes enables changes in the structure and function of ecosystems to be monitored, leading to implementation of forest conservation and management programs (Behera et al. 2012).

All the microenvironmental factors observed (except for pH) are correlated with changes in the composition and structural values of tree and shrub species in the *Fagus* forests of the state of Hidalgo. The results obtained here are important because they can serve as a reference for determining how and to what extent particular changes in microenvironmental conditions are related to the composition, structure and dynamics of *Fagus* forests. A large number of studies carried out in different ecosystems and regions have shown that vegetation is highly sensitive to microenvironmental changes in the amount of light, moisture and air temperature and soil (Davies-Colley et al. 2000), which, in turn, tend to vary in forests due to differences in exposure, slope, topography (Gehlhausen et al. 2000; Xu et al. 2004), gaps in the canopy (Beckage and Clark 2003; Godefroid et al. 2006; Grau 2004), stage of succession, degree of fragmentation (Bunyan et al. 2012; Nunes and Maës 2006), changes in land use to agriculture, pasturing, forest use (Chen et al. 1999; Ledo et al. 2009; Ortiz-Quijano et al. 2015) and climate change (Chmura et al. 2011; Téllez-Valdés et al. 2006; Rowden et al. 2004), among others.

Natural or anthropogenic disturbances, by modifying rates of growth, mortality and distribution of plant species, also alter the microenvironmental conditions in ecosystems. The El Gosco locality serves as a practical illustration of this: in recent years the residents of villages near the *Fagus* forest at this locality have gradually begun to extract trees for firewood, mainly *Quercus* spp. and to a lesser extent *Fagus*. As a result, the composition of the canopy has changed and the structural values of the species at this locality have become different from those at the other localities, where there is no evidence of disturbance of a similar magnitude (Ortiz-Quijano et al. 2015, 2016). At this locality, the microenvironmental variables had the lowest values for amount and depth of litter, soil moisture and tree cover, and the highest values for soil temperature. At the other localities, the ranges of variation in the biotic and abiotic characteristics analyzed were lower, so they can probably serve as references in management and conservation programs as the ‘typical’ microenvironmental and structural conditions of *Fagus* forests of Mexico.
Recent studies on the environmental history of beech forests (Ortiz-Quijano et al. 2015) and on the population structure of F. grandifolia subsp. mexicana (Ortiz-Quijano et al. 2016) in the state of Hidalgo indicate that the range of variation in environmental conditions has remained stable in most of these forests, at least over the last 100 years, in terms of the scale, frequency and duration of small scale natural disturbances. Although microenvironmental variations were estimated from only one year of sampling, growth ring analysis of F. grandifolia subsp. mexicana did not show any significant trends of environmental change (Ortiz-Quijano et al. 2015). Thus the variation found in floristic composition and in species structural values between Fagus forests of Mexico (Hidalgo, Tamaulipas and Veracruz) could be interpreted as an indicator of differences in microenvironmental conditions, considering that local changes in the composition and structure of vegetation are the result of population responses to environmental variations (Behera et al. 2012; Bunyan et al. 2012; Nunes and Maës 2006) and vice versa. It should be noted that the composition and structure of a plant community is considered to be a product not only of local physical conditions and interactions between species but also of regional differences such as climate, and of historical processes such as speciation, dispersal, migration and extinction (Ohmann and Spies 1998).

Unlike other forests in the Americas, Asia and Europe whose canopy is dominated by a Fagus species, a key characteristic of the Mexican beech forests is that they grow in a subtropical or warm temperate climate and are the most southerly beech forests in the northern hemisphere (located at 21° latitude; Ortiz-Quijano et al., 2016; Peters, 1997; Pignatti et al. 2006). This makes them a special type of plant association whose precarious existence in the present day is evidence of plant migration patterns due to climate changes in the recent geological past.

ACKNOWLEDGMENTS

This study had scientific support from a Ciencia Básica project of the Consejo Nacional de Ciencia y Tecnología: ‘Estructura, diversidad de especies vegetales y distribución actual de los bosques de haya (Fagus grandifolia subsp. mexicana) en el estado de Hidalgo, Mexico’, with the number CB-2011/169141. The authors acknowledge the comments and suggestions of four anonymous reviewers, which contributed to substantially improving this article.

REFERENCES


Peña L, Amezaga I, Onaindia M (2011) At which spatial scale are regional and local scale heterogeneity. Rural Areas, Forestry and Fisheries, 78–87.
