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Affinity among mountain ranges in Megamexico: A phytogeographical scenario

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Abstract

The concept of Megamexico as a phytogeographic unit has been introduced by Rzedowski (1991) on the basis of distribution patterns of genera. Until now precise information on the resemblance between plant communities in the proposed Megamexico was scarce. This phytosociological study documents the affinities between plant communities within Megamexico, based on studies from mountain ranges in Mexico (Sierra Chichinautzin, Sierra Nevada) and Guatemalan mountain ranges (Sierra de los Cuchumatanes, Cadena Volcánica). Data, collected in the style of Braun-Blanquet during extensive fieldwork, were pooled into a single data set, and analyzed by using (1) TWINSpan, for plant community classification, (2) ordination (DCA), (3) alpha log series biodiversity–index to measure intergroup diversity, and (4) information on the altitudinal distribution of the vegetation belts. Classification showed that four communities were common to the two groups of mountain ranges, namely, alpine bunchgrassland, pine forest, fir forest and mixed forest. Along the altitudinal gradient Mexican communities are distributed 200 m higher than their Guatemalan equivalents. This appears to be an illustration of the ‘Massenerhebungseffekt’. DCA showed that the first axis represents a set of minor differences of closely related ecological factors (e.g., temperature, precipitation) and the second a humidity gradient. The biodiversity index showed that the Mexican mixed forest was significantly more diverse than the Guatemalan mixed forest. From the present results, ecological conditions among mountain ranges in Megamexico differed significantly. To conclude, phytogeographical units in Megamexico can better be defined on basis of both historical and ecological characteristics of the communities.

Abbreviations: community refers to plant community throughout the paper.

Nomenclature: For vascular plants in Mexico: Rzedowski & Rzedowski (1981, 1985, 1991) and for Guatemala: Standley *et al.* (1946–1976); mosses for Guatemala: Bartram (1949).

Introduction

Phytogeographical research carried out in recent decades has underlined the strong floristic affinity between Mexico and Guatemala (e.g., Steyermark 1950; Knapp 1965; Rzedowski 1978; Gentry 1982; Rzedowski 1991). In particular, similarity between these two regions has been documented at the generic level and led to the ‘Megamexico’ concept of Rzedowski (1991). He stated that the area between northern Mexico/southern USA and the Depression of

Nicaragua is to be considered an authentic phytogeographical unit and it represents an area of very high proportion of endemisms. This statement suggests that similar historical events govern the chorology of plant genera in both regions. A phytogeographical unit, however, should also share similar responses of communities to ecological factors (Brown 1988; Myers & Giller 1988). In other words, plant assemblages from different areas within a certain phytogeographical unit should not differ significantly in their response to historic events and ecological factors. Under this view,

the authors hypothesized that plant communities can be used as indicators to document ecological affinity within a biogeographic unit. Otherwise, the scope of this paper is to compare the ecological (dis) similarities of common communities of Megamexico.

Mountain ecosystems provide an ideal situation to compare floristic affinities because most zonal vegetation types (*sensu* Walter 1986) found in high mountains of Mexico are present in the high ranges of Guatemala. Mountain ranges of comparable elevation as the ones present in Mexico and Guatemala are not found in Honduras, Nicaragua and El Salvador, so that Guatemala represents the meridional limit of the temperate-based mountain flora. Also, according to Rzedowski (1991), the distribution patterns of the communities found on Mexican and Guatemalan high mountain ranges may be determined by similar ecological conditions.

Lauer & Frankenberg (1978), by studying the distributions of the main plant communities of Central Mexico in relation to climatological factors, found that temperature and precipitation explain the biogeographic distribution pattern best. These results were obtained by inferring correlation between present vegetation types and data from climatological stations. Lauer & Frankenberg (1978) studied the way climatic factors relate to vegetation (top-down approach). However, another approach is to investigate the way communities respond to ecological factors (bottom-up approach). To test the authenticity of Megamexico as well as Lauer's findings, further information on floristic composition of communities and their distribution is urgently needed. Detailed documentation, however, for all zonal Mexican and Guatemalan communities (structure and floristic composition) is not yet available for all habitat types. Recent phytosociological surveys have been carried out in Mexico (Sierra Chichinautzin, Sierra Nevada) and in Guatemala mountain ranges (Sierra de los Cuchumatanes and Cadena Volcánica).

Based on this information, the purposes of the present study are twofold: to document the actual floristic and ecological affinity of Megamexico and to seek for underlying ecological factors influencing the distribution of the corresponding zonal communities. This is the first study, using quantitative methods, dealing with Guatemalan high mountain communities being classified and compared with Mexican ones.

Study area

The geographical position of the study area is shown in Fig. 1. The study area includes the second highest peak of Central Mexico, Popocatepetl volcano (5465 m) and the highest peak of Guatemala, Tajumulco volcano (4220 m). The Sierra de los Cuchumatanes in northwestern Guatemala with its highest peak at 3800 m differs from all other three sites by being of nonvolcanic origin. The elevation of the study areas in Guatemala goes from 3000 to 4200 m and in Mexico from 2600 to 4300 m. Anthropogenic activities, especially in the last thirty years, have reduced the natural forests drastically in both mountain regions (Perfil Ambiental 1987; Velázquez 1993). Climate in both regions has two main seasons: rainy (May-October) and dry season (November-April).

Methods

Data from 230 relevés (collected in the style of Braun-Blanquet 1951) from undisturbed sites in Mexico and Guatemala were used (132 Mexican and 98 Guatemalan) for this study. In total 480 different plant species, including phanerogams, ferns and mosses, were identified. Species data were used in this analysis because they are indicative of ecological conditions in contrast with other higher taxa. By using species data, however, more variation is introduced in the analysis. As a consequence, interpretations may be oversimplified. Considering the genera exclusively, the overall similarity between Mexico and Guatemala is about 95%.

The representative size of the sampling unit varied with vegetation type: forests (625 m²), shrubland (200 m²), grassland (125 m²) and alpine bunchgrassland (30 m²). To compare the percentage of cover per species per relevé, the aerial cover values estimated in the field were converted into the Van der Maarel (1979) scale. The relevés from Mexico and Guatemala were pooled into a group and ten communities were identified by using a divisive classification method (TWINSPAN, Hill 1979). For our purpose five cut levels were sufficient to obtain a phytosociological classification at community level. Six different Guatemalan communities are distinguished and are described shortly in this paper. Full descriptions of the Mexican community groups is provided by Velázquez (1993). To give an overview the characteristics of the communities common to both regions a table was prepared (Table 1).

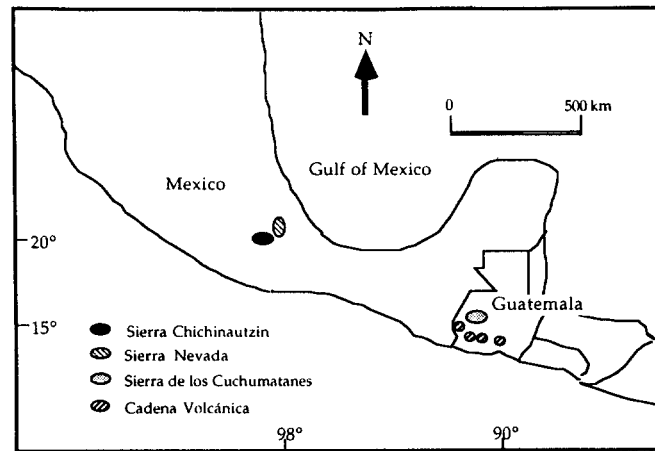


Fig. 1. Study areas in Mexico and Guatemala.

Until now no exhaustive phytosociological survey is available for other vegetation zones (e.g., the lowlands) of Guatemala and Mexico, therefore no phytosociological nomenclature was used for the present study.

If the Megamexico proposal is acceptable at community level, no significant differences in ordination of common vegetation types is expected. According to this hypothesis a theoretical ordination diagram was sketched (Fig. 2). This was investigated by using detrended correspondence analysis (Hill & Gauch 1980; CANOCO 3.0 program package, Ter Braak 1988). Moreover, this analysis helped to elucidate the possible ecological factors influencing the distribution of the common communities from the study area. This ordination method computes scores per species and relevés along axes. The relevé scores per community were treated as a group and the mean and standard deviation were calculated for the first and second axis. The results of this procedure were used to make a graphical representation of the detrended correspondence analysis-ordination outcome. Furthermore, significant differences between common communities were obtained by comparing the confidence limits of the relevé scores from both axes (Sokal & Rohlf 1987) (Table 2).

Logarithmic series biodiversity index was calculated for all common communities present in the study area by using the program LOGSERIE (Krebs 1989). This index was chosen because of three reasons, namely, common communities contain comparatively few species that are common and large numbers of species that are rare, the relevés were not selected at random and this index is not influenced by sample size (Magurran 1988). In addition, other studies aimed at comparing species diversity concluded that this index was the

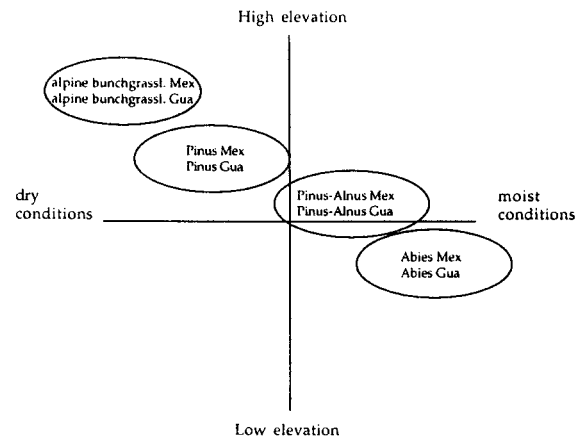


Fig. 2. Representation of the expected ordination diagram.

best measurement (Krebs 1989; Magurran 1988; Wolda 1983). Chi-squared goodness of fit test (Sokal & Rohlf 1987) was used to determine (dis)similarities in biodiversity index between common communities. A level of $P < 0.05$ was considered as significant throughout the analysis.

Results

By Twinspan classification analysis ten communities were distinguished, which are shown in a dendrogram (Fig. 3). The first division split Mexican and Guatemalan communities clearly (eigenvalue $\lambda = 0.782$). Regarding the Mexican communities, fir forest was the most different at the second division and in Guatemala the alpine bunchgrassland. After five

Table 1. Review of Mexican and Guatemalan common communities.

Characteristics	Mexico		Guatemala	
Locations	S. Chichinautzin	Sierra Nevada	Cadena Volcánica	Sierra de los Cuchumatanes
Origins	Pliocene-Quaternary	Pliocene-Quaternary	Pliocene-Quaternary	Cretaceous
Dominant soil type	Lithosol	Andosol	Andosol	Luvisol
Climate (Koeppen)	Cw	Cw	Cw	Cw
Mean precipitation (altitude)	950 mm (3000 m)	1187 mm (3550 m)	1475 mm (3000 m)	1270 mm (2500 m)
Common vegetation types	No alpine vegetation	Alpine bunchgrassland 4000–4300 m Regosol <i>Calamagrostis toluensis</i> – <i>Lupinus montanus</i> – <i>Lupinus montanus</i> <i>Arenaria bryoides</i> – <i>Festuca livida</i>	Alpine bunchgrassland 3900–4200 m Regosol <i>Lupinus montanus</i> – <i>Calamagrostis vulcanica</i> <i>Luzula racemosa</i> – <i>Arenaria bryoides</i>	No alpine vegetation
	Pine forest 2900–4000 m shallow soils <i>Muhlenbergia quadridentata</i> – <i>Pinus hartwegii</i> <i>Festuca toluensis</i> – <i>Pinus hartwegii</i>		<i>Lachemilla vulcanica</i> – <i>Pinus hartwegii</i>	Pine forest 3000–3900 m shallow soils <i>Hypnum spp.</i> – <i>Juniperus standleyi</i> <i>Thuidium delicatulum</i> – <i>Pinus hartwegii</i>
	Fir forest 2400–3600 m soils very thick/steep slopes <i>Senecio angulifolius</i> – <i>Abies religiosa</i> <i>Senecio barba-johannis</i> – <i>Abies religiosa</i> <i>Alnus firmifolia</i> – <i>Abies religiosa</i>			Fir forest 2800–3400 m soils very thick/steep slopes <i>Thuidium delicatulum</i> – <i>Abies guatemalensis</i>

Table 2. Significance table for the first and second axis of the ordination.

	Axis 1 ($\lambda = 0,836$) set of factors	Axis 2 ($\lambda = 0,543$) humidity	
Mexico			Guatemala
Alpine bunchgrassland	*	*	Alpine bunchgrassland
Pine forest	*		Pine forest
Fir forest	*		Fir forest
Mixed forest	*		Mixed forest

* P > 0,05.

divisions a similar pattern was encountered for both Mexican and Guatemalan vegetation types.

The differences among Guatemalan fir, juniper-pine and pine forest are less pronounced than the correspondent Mexican communities.

Detailed information about the Mexican communities is available (Velázquez 1993), whilst Guatemalan communities are still poorly known. Consequently, a short description of the common communities is given

below in descending elevational order, according to Islebe (unpubl.).

Alpine bunchgrassland

Lupinus montanus – *Calamagrostis vulcanica* community

Physiognomy. Tussock grass species up to 1 m high. Two dominant layers are present: (1) grass layer

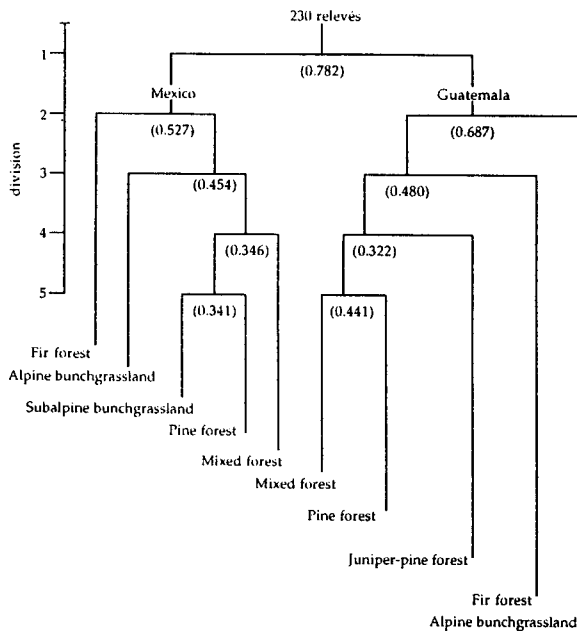


Fig. 3. Dendrogram based on Twinspan classification.

dominated by *Calamagrostis* and (2) groundlayer with mosses such as *Breutelia* and *Leptodontium*.

Floristic composition. Diagnostic species are *Lupinus montanus*, *Luzula racemosa*, *Gnaphalium salicifolium* and *Potentilla heterosepala*.

Environmental characteristics. Community on gentle slopes at wind-protected sites. Soils are Regosols.

Luzula racemosa – *Arenaria bryoides* community

Physiognomy. Open vegetation with one dominant groundlayer. *Arenaria bryoides* forms cushions. On rocky outcrops *Racomitrium crispulum* is dominant.

Floristic composition. Diagnostic species are *Luzula racemosa*, *Agrostis tolucensis* and *Draba vulcanica*.

Environmental characteristics. Community found on steep slopes and sites exposed to wind, solar radiation and temperature fluctuations.

Pine forest community group

Hypnum spp. – *Juniperus standleyi* community

Physiognomy. Open vegetation with four different layers: (1) tree layer, consisting mainly of *Pinus hartwegii* and *Juniperus standleyi*, up to 25 m high; (2) shrub layer consisting mostly of *Juniperus standleyi* and *Holodiscus argenteus*; (3) herb and bunch-

grass layer consisting principally of *Oxylobus glanduliferus*, *Agrostis tolucensis* and *Calamagrostis junciformis*; and (4) ground layer consisting mainly of *Hypnum* spp., *Thuidium delicatulum* and *Lachemilla vulcanica*.

Floristic composition. Diagnostic species are: *Juniperus standleyi*, *Pinus hartwegii*, *Hypnum* spp., *Agrostis perennans*, *Werneria nubigena* and *Calamagrostis junciformis*.

Environmental characteristics. This community can be found between 3100 and 3800 m, preferably on undulating slopes, where soils (Luvisol) are shallow. *Lachemilla vulcanica* – *Pinus hartwegii* community

Physiognomy. Coniferous forest consisting of three layers: (1) tree layer up to 20 m high; (2) herb bunchgrass layer with *Lupinus montanus* and *Calamagrostis vulcanica*; and (3) ground layer dominated by *Lachemilla vulcanica*.

Floristic composition. The diagnostic species are *Lachemilla vulcanica*, *Calamagrostis vulcanica*, *Senecio oerstedianus*, *Luzula gigantea* and *Poa tacanae*.

Environmental characteristics. This forest type occurs on steep slopes between 3300 and 3900 m.

Mixed forest

Thuidium delicatulum – *Pinus hartwegii* community

Physiognomy. This community is made up of four layers: (1) tree layer consisting of *Pinus hartwegii* and *Alnus firmifolia*; (2) shrub layer consisting of *Baccharis vaccinoides*; (3) herb layer dominated by *Agave hurteri*; and (4) ground layer with mosses (*Thuidium*).

Floristic composition. Diagnostic species include *Eryngium carlinae*, *Agave hurteri*, *Baccharis vaccinoides*, *Hypnum* spp., *Alnus firmifolia* and *Pinus hartwegii*.

Environmental characteristics. This community is found on flat areas, between 2900 and 3200 m, where soils are shallow.

Fir forest

Thuidium delicatulum – *Abies guatemalensis* community

Physiognomy. Dense forest with trees up to 30 m. Three dominant layers are present: (1) tree layer dominated by *Abies guatemalensis*; (2) shrub layer with *Roldana barba-johannis*, *Tetragyron orizabensis*; and (3) a ground layer with mosses (*Thuidium delicatulum*).

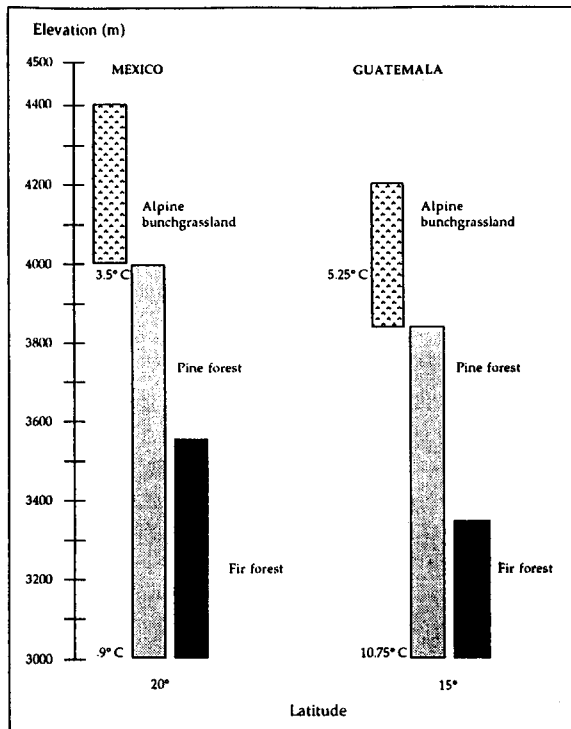


Fig. 4. Elevational distribution of Mexican and Guatemalan common communities.

Floristic composition. Diagnostic species are *Fuchsia microphylla*, *Senecio callosus*, *Trifolium amabile*, *Sabazia pinetorum* and *Pinus ayacahuite*.

Environmental characteristics. Forests on very steep slopes occurring between 2800 and 3400 m, where soils are thick with rich organic matter.

The altitudinal distribution of the common communities above 3000 m is shown in Fig. 4. Three vegetation types can be distinguished along an altitudinal gradient for both study areas, namely: alpine bunchgrassland, pine forest and fir forest. Mixed forest altitudinal distribution extends below 3000 m and overlaps with pine forest belt. The upper limits of the Guatemalan vegetation belts are situated 200 m lower than those of the Mexican ones.

The ordination diagram of the relevés obtained by DCA is shown in Fig. 5. A high Eigenvalue ($\lambda_1 = 0.836$ and $\lambda_2 = 0.543$) of the first axes suggests a marked separation between relevés pooled into communities. In the ordination diagram a clear segregation along the first axis was found between Mexican and Guatemalan communities. Conversely, common communities to both regions were positioned at equivalent

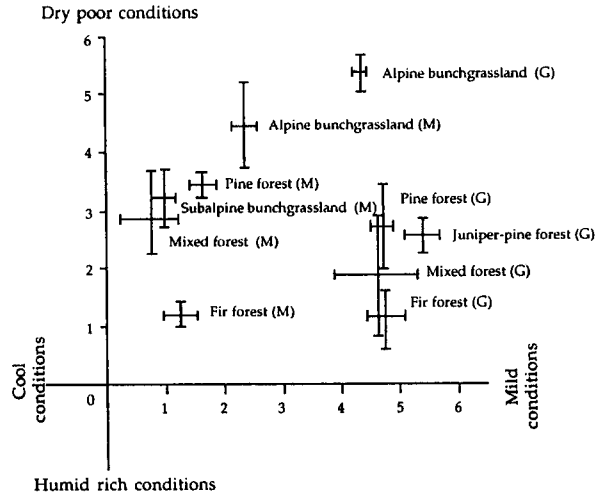


Fig. 5. Representation of the DCA ordination diagram.

locations along the second axis. Alpine bunchgrassland communities from both regions were positioned on the upper extreme of the second axis, whereas fir forest on the lower extreme of the diagram. This suggests that the second axis represents a humidity gradient where drier conditions are typified at the upper extreme (Fig. 5). In short, Mexican and Guatemalan common communities react similarly to the ecoclimatological factor(s) indicated by the second axis.

There is a clear segregation between Mexican and Guatemalan communities along the first axis (Fig. 5). In our compound ordination diagram the first axis does not seem to be correlated with one particular climatic or ecological factor. Taking into account that anthropogenic activities were excluded, only historical events or ecological factors ought to correlate to this first axis. However, unlike ecological factors, historical events in Central American regions have influenced the communities in a similar way (Graham 1976, 1989). As a consequence, ecological factors are considered the only source of variation to explain this segregation. Notwithstanding, minor differences in ecological (climatic) factors between both regions are documented. To illustrate this further, precipitation, temperature, competition, soil types, among other factors, are not entirely the same in both regions (Fig. 4; Table 1). To summarize, the first axis represents probably a set of factors (e.g., precipitation, temperature, competition and soil differences), where every factor contributes, in part, to explain the total difference between Mexican and Guatemalan species assemblage.

In Table 2 (dis)similarities between Mexican and Guatemalan communities were integrated. All common communities differed significantly if compared along the first axis. In addition, alpine bunchgrasslands in Mexico and Guatemala are different according to both axes.

The Alpha (α) log series biodiversity index (Krebs 1989) computed for all communities is given in Fig. 6. The only community that differed significantly from its equivalent was the mixed forest, being the Mexican mixed forest more diverse. The difference in successional stage between Mexican and Guatemalan mixed forests as well as the larger human impact in Guatemala than in Mexico may be the causes of this contrast.

Discussion and conclusions

In both Guatemalan and the Mexican mountain ranges studied five main vegetation types are present (Fig. 3). The Mexican subalpine bunchgrassland is not present in Guatemala, whereas the Guatemalan juniper-pine forest is not found in Mexico. In other words, four out of the five main vegetation types present in each of the regions are in common (Fig. 3). Under this view, the main vegetation types-deduced from classification analysis-of both regions show a resemblance of ca. 80%, with 10% endemic to Mexico and 10% to Guatemala. The uncommon Mexican subalpine bunchgrassland is probably man-induced because the areas concerned have been used frequently for livestock for many years (Velázquez 1993). The human-impact at the present is, in the vast majority of the areas, inconspicuous, but the historical effect may still be noticeable. Unlike the Mexican situation, the Guatemalan juniper-pine forest represents ecological conditions common in Guatemalan mountains so that this vegetation type may be considered zonal. In brief, at community level similarities were found, presenting comparable distribution patterns in their respective mountain range and differences in floristic composition.

The common pattern of distribution between the Mexican and Guatemalan community groups may be caused by a humidity gradient (Fig. 5). Previous research (Velázquez 1993) has shown that analogous distribution patterns of the Mexican vegetation types are correlated with humidity (first axis) and elevation (second axis). In our specific study it is difficult to interpret ordination trends in terms of gradients. In the present study the second axis resembles the first axis of Velázquez (1993) and explains a large percentage of the

total variation of all – Mexican and Guatemalan – communities (Axis 2, $\lambda = 0.543$). Conversely, the largest variation (Axis 1, $\lambda = 0.836$) of the data set seems not to be correlated with one specific ecological factor, but a complex of them (see below for further explanation). This discrepancy was observed in the classification outcome (dendrogram, Fig. 3) and it was elucidated by the first axis of the ordination diagram (Fig. 5). Otherwise, the influence of this set of factors shows differences along a geographical gradient, introducing an altitudinal and a latitudinal ecocline (Fig. 4). We assume that the first axis is correlated with a temperature gradient in north-south direction, being Mexico relatively cooler than Guatemala. Furthermore, the distribution of communities in Sierra Chichinautzin was attributed to temperature rather than precipitation for the second axis (Velázquez 1993). The influence of this temperature gradient could be further overlapped with other ecological factors such as, precipitation, water availability, soil type, competition and geological history.

Fig. 4 shows that Mexican and Guatemalan communities from the study area differ in their altitudinal distribution. Guatemalan community groups are located ca. 200 m lower than their Mexican equivalents. According to the lapse rate reported for the Mexican region (0.5–0.6 °C per 100 m altitudinal difference) by Lauer & Klaus (1975) the corresponding Guatemalan vegetation groups are distributed in areas with temperatures ± 1.7 °C warmer. Two major causes may be responsible to the different altitudinal distribution of these common vegetation types: Guatemala is closer to the Equator and the ‘Massenerhebungseffekt’ is more evident in Mexico (Grubb 1971; Hastenrath 1963). The lack of representative meteorological stations in the mountainous zones of the whole study area made the interpretation regarding this subject rather complex, thus only general trends could be extrapolated.

Lauer & Klaus (1975) found that frost occurs ca. 200 days per year near the treeline (4000 m, *Pinus hartwegii* vegetation) at the Pico de Orizaba. In addition, the effects of northern arctic cold air intrusions between December and March, known as ‘nortes’ in Mexico and Guatemala, are more intense in Central Mexico than in Guatemala. Personal observations in Guatemala indicate that at 3800 m elevation in the Sierra de los Cuchumatanes frost only occurs between November and February, and the coldest months are January and February (-4° and -5° °C, lowest measured temperatures, respectively). Thus, water availability – mainly determined by the number of frost

days – in the upper pine and alpine bunchgrassland community groups is less restricted in Guatemala.

There is a general gradient in precipitation between Central Mexico and Guatemala, the first being relatively drier than the latter. The annual mean precipitation for the studied Mexican area is about 800 mm (Rzedowski 1978), whereas for the Guatemalan area about 1100 mm (Perfil Ambiental 1987). Furthermore, soil differences are especially important in Sierra de los Cuchumatanes where soils are poor in the organic layer. The Cadena Volcánica of Guatemala shows similar soil types (Andosols) as the ones of Sierra Nevada (Popocatepetl and Iztaccíhuatl) and their cones are of similar geological age, suggesting a similar time of plant colonization. In contrast, cooling events and glacial formations took place during the last glacial at the Mexican study area (Ohngemach & Straka 1983), as well as in Sierra de los Cuchumatanes (Hastenrath 1974), but not in the highest peaks of the Cadena Volcánica (Hastenrath 1963). This implies that the maximum elevation of Cadena Volcánica was reached after the last glacial and is of Holocene age.

The relative compactness of the Guatemalan *Abies* community in comparison with the Mexican one (600 m altitudinal range in Guatemala and 1200 m in Mexico) is remarkable. One possible explanation for this phenomenon could be the intensive and uncontrolled logging activities done to fulfill the demand of *Abies guatemalensis* wood and the agricultural use in this vegetation zone. Nowadays, *Abies guatemalensis* is considered an endangered species in Guatemala. From the successional point of view, Velázquez (1993) states that *Abies religiosa* and *Pinus hartwegii* are the original zonal communities of the Sierra Chichinutzin. Hence, Mexican and Guatemalan mixed forests are considered, in most of the cases, successional stages of the *Abies* forest. Therefore, fir forests could have been much more extended in earlier times. Human interference in the past still influences the extension of the present communities.

In the scope of the present study the Mexican mixed forest is the only community that turned out to be more diverse than the Guatemalan mixed forest. This contrasts with the general pattern of diversity increasing towards the Equator (Brown 1988). This result may be explained on basis of the maturity stage of the mixed forest because in both regions it is considered as successional between pine and fir forest, the latter being the climax situation (Rzedowski 1978). In the Guatemalan mixed forest species such as *Lachemilla*, Ericaceae, *Pinus*, are more common, whereas species

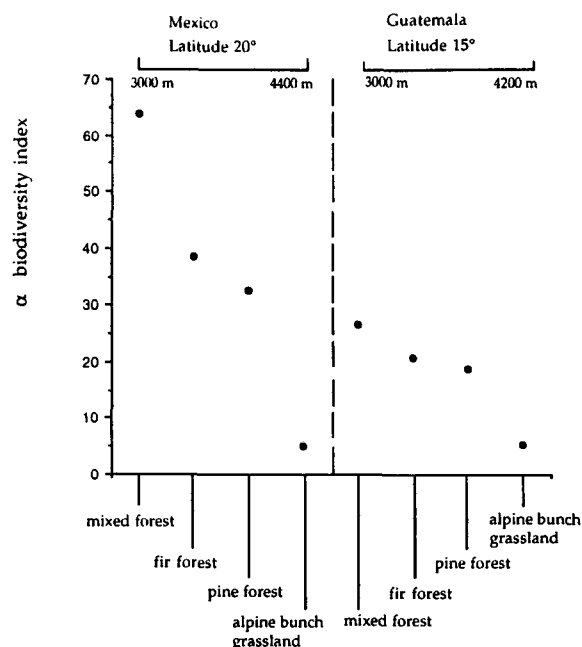


Fig. 6. Alpha log series biodiversity index for Mexican and Guatemalan shared communities.

disturbance-indicators such as *Lupinus*, *Cirsium*, *Pentstemon*, *Eryngium*, *Senecio* and *Ribes* are more abundant in the Mexican mixed forest. This suggests that the Guatemalan mixed forest is probably in a more advanced successional stage than the Mexican mixed forest. Additionally, intensive human impact, such as overgrazing and trampling, is substantially larger in Guatemalan highlands than in Mexico. This is further illustrated by the considerably small differences in diversity between the Guatemalan mixed forest and Guatemalan fir forest, which is not the case for the Mexican situation (Fig. 6).

What implication do we have for the phytogeography of the mountainous regions? Similar communities have different local diagnostic species, implying local biotic and abiotic differentiating factors. From the present results, ecological conditions among mountain ranges in Megamexico differed significantly. In the present study, related vegetation types, treated independently, constitute a similar pattern in historical and ecological perspectives. Nevertheless, the floristic assemblage between common communities from Mexico and Guatemala differs significantly as observed by the segregation along axis one (Fig. 5). In this context, it is hypothesized that this first axis represents the ecological biogeographical level. In this view, the pro-

posal of Megamexico (Rzedowski 1991) as an useful phytogeographical unit fits only within the historical biogeographic pattern. This is corroborated by comparing both regional patterns at major taxonomic levels such as genera and families. To provide an example, *Abies* forest should be divided into a northern and a southern element, so that more appropriate terminology is achieved. In this way, Megamexico can be split in concise historical and ecological subunits. The inherent variability of stands of given community types presents some difficulties in testing phytogeographical affinities of larger geographical areas. Significant differences in, for instance, soil properties may influence the total floristic variation. However, with species data a higher ecological resolution is achieved, which cannot be accomplished with higher ranked taxa. To conclude, phytogeographical units in Megamexico can better be defined on basis of both historical and ecological characteristics of the communities.

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