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INSULAR BIOGEOGRAPHY OF SUBMONTANE HUMID FORESTS IN MEXICO

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The Mesoamerican area, located between 12° to 32° North Latitude, includes communities with a very characteristic flora and fauna. Areas with xerophytic vegetation and the humid submontane forests are the most important in showing a high degree of endemism (Figure 1). The taxonomic level of endemics for xerophytic areas reaches a high rank and their relative proportion exceeds that in humid montane forests because there are many autochthonous genera and it is possible to find endemic families.

For the submontane humid forest communities, the characteristic lineages are frequently at the species level, although sometimes we can find endemic genera and tribes. This is explicable by the particular biogeographic history and ecological conditions of that region.

Desert and semidesert areas of Mesoamerica, including the caducifolious tropical forest (sensu Rzedowski, 1978), have received preferential treatment in floristic, faunistic and biogeographical research. On the other hand, humid montane areas have received less attention. This may be explained at least in part because of the difficulties of access to some places in the mountains and the difficult working conditions. Fortunately, in the last decade these impediments have been decreased, at least in areas of southern and western Mexico.

The distribution of submontane areas with high precipitation in Mexico is discontinuous, because the physiographic, climatic, and vegetational barriers hinder the free dissemination of elements of stenotopic montane humid forest (sensu Rzedowski, 1978) present in those areas.

The submontane humid forest is found in altitudinal intervals between 900 and 1800 meters (submontane), in montane locations protected from high insolation, deep slopes that receive and keep moisture (often more than 2000 mm), and where the dominant climates are moist warm and humid (Am and Cf of the Köppen classification). This set of ecological conditions occurs only in some parts of the several Mesoamerican mountain ranges, while in other areas different conditions act as barriers. In terms of communities and altitudinal levels, the tropical and oak forests and scrubs exclude a great number of submontane mesic elements that seldom occur below 900 meters altitude. The high altitudinal pine-oak forests and coniferous forests establish the upper boundary of the mesophilous montane forest.

For the purpose of this report, we define the submontane area as one that is located on some Mesoamerican ridges and supports forests with the features

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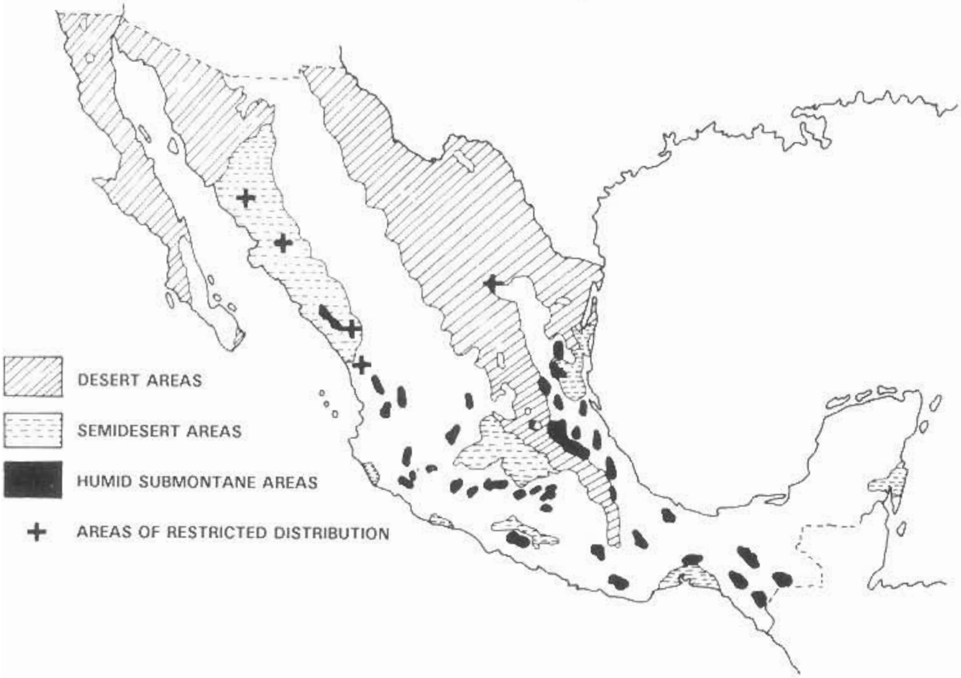

Figure 1. Map showing humid submontane and xeric areas of Mexico.

mentioned previously, namely: a) altitude of 900-1800 meters, b) protected from insolation (slopes and gorges), c) deep slope, d) high moisture levels (2000 to 6000 mm), and e) warm-temperate and temperate very humid climates.

Although there are some important topics about the botanical characterization of the community of our interest, we refer those interested in floristic, vegetational, and phytogeographical considerations to the work of Luna (1984), who recently made a good synthesis of these and other aspects of mesophilous montane forests. The areas defined in this way form an intracontinental archipelago located on the sierras of Mexico south of 24° North Latitude. Luna (1984) and LLorente (1984) have distinguished the distribution of submontane islands (Figure 2). Even in these islands the mesophilous forest is not distributed continuously, but occurs only in very humid sites with a rough physiography. Generally speaking, each island is a physiographic unit.

We propose the archipelago as a model for our biogeographical work. Possibly the fauna of these islands developed by vicariant events instead of dispersal of colonization. Inherent in the archipelago model is the hypothesis that stenotypic elements in the community will differ at the specific and subspecific levels. This will be true for those taxa where altitudinal intervals are narrow, e.g., 1400-1700 or 900-1400 meters.

The islands are often occupied by elements that Halffter (1978) included in the Montane Mesoamerican Pattern. This author cited the Guatemalan and Chiapas highlands as the center of origin and diversification of autochthonous elements of Mesoamerica that belong to the pattern mentioned. Submontane

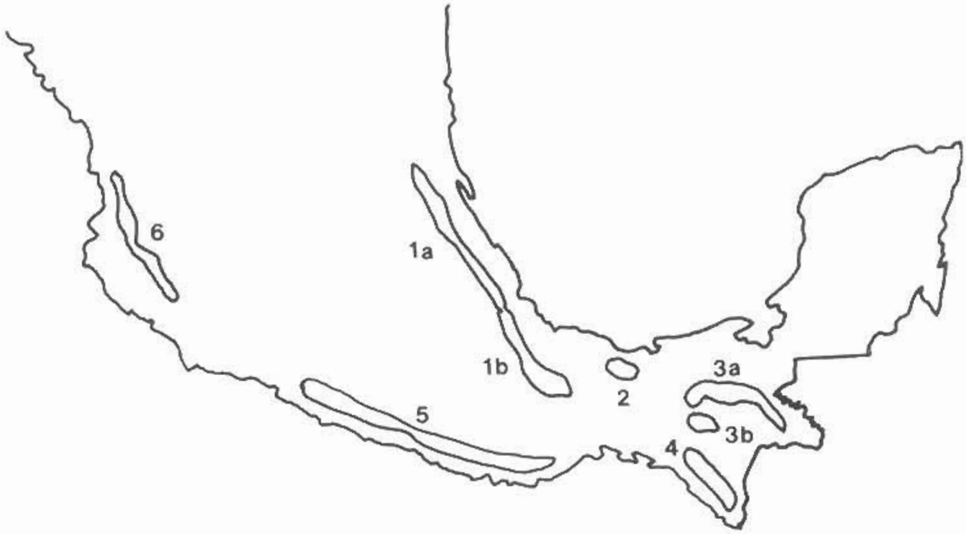

Figure 2. Map showing location of submontane islands in Mexico. 1a = Sierra Madre Oriental. 1b = Sierra de Juárez. 2 = Los Tuxlas, Veracruz. 3a = Vertiente Atlántica de Chiapas. 3b = Chiapas, centro. 4 = Chiapas, Vertiente Pacífica (Soconusco). 5 = Oaxaca-Guerrero. 6 = Nueve Galicia.

areas of southern Mexico (Chiapas, Oaxaca, and Guerrero) contain the highest numbers of endemics, including those of high taxonomic rank. Furthermore, those areas are located in the geologically more suitable and older sierras of Mexico: Macizo Central de Chiapas, Sierra Madre del Sur, and Sierra de Juárez.

We have been working for five years on montane "islands" at Nueva Galicia and Oaxaca-Guerrero in southern and western Mexico. These islands are located on the Pacific slope south of the Sierra Madre Occidental, the west extreme of the Eje Neovolcánico and the Sierra Madre del Sur. From each of these islands, we have obtained information on butterflies and birds and have done intensive collecting along altitudinal transects. At Nueva Galicia we explored west central Nayarit (Sierra de San Juan), and at Oaxaca-Guerrero island, the Sierra de Atoyac in Guerrero.

For the Nueva Galicia island, the archipelago model has confirmed the predictions because we notice, for butterflies, seven subspecies stenotopic to mesophilous forest that are endemics: *Dismorphia amphiona lupita, Diaetheria asteria, Pereute charops* ssp. nov., *Papilio garamas* ssp?, *Papilio victorinus* ssp. nov., *Consul electra* ssp. nov., and *Euselasia aurantiaca* ssp. nov. Five of them are new to science. They occur between 600 and 1200 meters elevation; the inferior displacement of the altitudinal interval may be due to a latitudinal effect.

Based on literature and collections, the subspecies cited are endemic to humid submontane areas between Colima and southern Sinaloa, that is, the submontane island of Nueva Galicia, whose southern boundary is the Balsas Depression. With the exception of *Diaethria asteria*, the other taxa reach only subspecific differentiation; these subspecies are most closely related to the Oaxaca-Guerrero ones.

Two endemic subspecies of birds are restricted to the submontane humid forest: *Thalurania colombica ridgwayi* and *Basileuterus culicivorus flavescens.* The most closely related subspecies of the latter is found in the Oaxaca-Guerrero island, that of the former occurs from Guatemala southward.

In the Oaxaca-Guerrero island the number of endemic taxa linked to the mesophilous forest is notably increased, more than 30 for butterflies and 10 for birds: *Actinote guatemalena guerrerensis, Eueides isabella nigricornis, Eunica augusta augustina, Archaeoprepona amphimachus baroni, Lieinix* sp. nov., *Pedaliodes* sp. nov., *Hypanartia dione* ssp. nov., *Adelpha* sp. nov., *Mesene margaretta* ssp. nov., *Pereute charops sphocra, Drucina championi* ssp. nov., *Morpho achilles guerrerensis, Dioriste tauropolis* ssp. nov., *Adelpha creton* ssp. *Actinote stratonice oaxaca, Fountainea eurypyle glanzi, F. rayoensis, Oleria zea diazi, Pteronymia artena praedicata, P. simplex timagenes, Greta annette moschion,* and *G. morgane morgane*, as examples of butterflies; *Dactylortyx thoracicus devius, Geotrygon albifacies rubida, Aulacorhynchus prasinus wagleri, Eupherusa poliocerca, Automolus rubiginosus guerrerensis, Cyanolyca mirabilis, Henicorhina leucophrys festiva, Basileuterus culicivorus* ssp., *Chlorospingus ophthalmicus albifrons*, and *Atlapetes brunneinucha suttoni* birds.

In Oaxaca-Guerrero there are 3 to 4 times more endemics in the mesophilous forest than in Nueva Galicia. Many of the subspecific taxa of butterflies are new to science, as expected. Nevertheless, their populations are local and often scarce. This coincides with their restricted altitudinal distribution between 1400-1700 meters, e.g., *Drucina championi* ssp. nov., and *Lieinix* sp. nov. In Oaxaca-Guerrero the number of endemic species is low. The most closely related subspecies are in the Guatemala and Chiapas highlands. The southern limits of distribution of the Oaxaca-Guerrero island are located in the Isthmus of Tehuantepec, a xeric and windy depression.

Some other endemic subspecies of south and west Mexico are not exclusive to one of the islands we studied, but are shared by Nueva Galicia and Oaxaca-Guerrero. These shared subspecies often are vicariants with those in the Gulf of Mexico slope, and Guatemala and Chiapas highlands. Those taxa are more euriecious because they are often present in other communities at lower altitudes, that is, from 0 to 1800 meters. They are less stenoecious to mesophilous montane forest, but are hygrophilic enough to be found only in the subcaducifolious tropical forest.

Some examples of subspecies of butterflies shared by the southern and western highlands are: *Lieinix nemesis nayaritensis, Myscelia cyaniris alvaradia, Catonephele cortesi, Epiphile adrasta escalantei, Pieriballia viardi laogore, Oxeoschistus hilarus* ssp. nov., *Parides erithalion trichopus, Episcada salvinia portilla, Pteronymia rufocincta, Euantia mazai diazi, Melinaea lilis flavicans* and others. We did not find similar patterns in birds.

A case of the whole (associated) variation of mimetic complexes is the so-called "Tiger Complex" composed in the south and west by *Dismorphia amphiona, Consul fabius, Melinaea lilis, Lycorea ceres* and some others with similar color patterns. They present the same equivalent modifications between the subspecies of the Gulf of Mexico and Chiapas with the western subspecies. One of those, *D. amphiona*, is the most stenoecious and has subspecies *lupita* in Nueva Galicia and *isolda* in Oaxaca-Guerrero.

Distributional Patterns (Table 1)

Using our own results and the distribution data from the literature and collections, we can characterize the patterns of distribution of the endemics of submontane hygrophilic conditions using 8 examples in the following scheme. The first 4 patterns include taxa present in all the submontane islands, except the fourth which is not yet known from Los Tuxtlas.

Pattern I includes subspecies with a wide range of distribution having peripheral populations taxonomically differentiated. This pattern is exemplified by *Consul electra electra* and *Euselasia aurantiaca aurantiaca* and its vicariants. The Balsas Depression barrier plays a determinate role in the taxonomic and geographic separation.

In Pattern II, the Isthmus barrier makes two group of islands (disjuncts?) each one having corresponding subspecies like *Episcada salvinia salvinia, Catonephele mexicana, Pieriballia viardi viardi, Eunica augusta augusta* and *Eueides isabella eva* and respective vicariants. The two latter do not reach the Nueva Galicia probably because of the presence of the Balsas region.

In Pattern III, the Isthmus and Balsas barriers act efficiently; but in the case of the Chiapas and western islands the populations of the northern and southern extremes are differentiated populations, as in the northern extreme of the Sierra Madre Oriental and Sierra Madre de Chiapas. These subspecies are more stenoecious, and have smaller altitudinal distributions than do the examples presented in patterns I and II.

Pattern IV is exemplified only by birds. The fragmentation of the archipelago occurs near the Isthmus of Tehuantepec for the northern and southern islands; on the other hand, through the south there are different subspecies for the Atlantic slope of Chiapas and in the Sierra Madre de Chiapas. The examples are: *Dactylortyx thoracicus* sspp. and *Henicorhina leucophrys* sspp.

The next four patterns exclude, at least, the Nueva Galicia island; it seems that the Balsas Depression played a subtractive role a long time ago; nevertheless it is necessary to further explore the central area, that is, the southwestern slope and the Fuego and Colima volcanoes. The possibility that the elements are of relatively new arrival to Mesoamerica can be excluded because some species, like *Papilio abderus* and *Dioriste tauropolis*, are old residents that have diversified in the Mexican mountains. Some other examples, like *Prepona deiphile* and others are probably recent arrivals.

Pattern V is exemplified by the butterflies *Mesene margaretta, Dioriste tauropolis*, and *Pteronymia artena*, and *Automolus rubiginosus* in birds. This pattern shows one subspecies in Oaxaca-Guerrero and another in the other islands. In this pattern, as in the following ones, the Isthmus of Tehuantepec is an important barrier. Some of the taxa representing this pattern are often found at the highest altitudinal limit of the subcaducifolious tropical forest, always above 700 meters altitude.

Pattern VI includes taxa that are very stenotopic to the mesophilous montane forest. There are three basic groups of subspecies: Guerrero-Oaxaca, Chiapas highlands, and Sierra Juárez-Sierra Madre Oriental. There is sometimes subspecific differentiation in Los Tuxtlas, Atlantic and Pacific slopes of Chiapas.

TABLE 1. Distributional patterns in humid submontane habitats, with examples of taxa. Numbered areas from Figure 2.

PATTERN I

Areas 1 - 5: *Consul electra electra*; *Euselasia aurantiaca aurantiaca*.
Area 6 only: *Consul electra* subsp. nov.; *Euselasia aurantiaca* subsp. nov.

PATTERN II

Areas 1 - 4: *Episcada salvinia salvinia*; *Catonephele mexicana*; *Pieriballia viardi viardi*; *Eunica augusta augusta*; *Eueides isabella eva*.
Area 5 only: *Eunica augusta augustina*; *Eueides isabella nigricornis*.
Areas 5 - 6: *Episcada salvinia portilla*; *Catonephele cortesi*; *Pieriballia viardi laogore*.

PATTERN III

Area 1a only: *Basileuterus culicivorus brasheri*.
Area 4 only: *Pereute charops* (*columbica* ?); *Basileuterus culicivorus ridgwayi*; *Geotrygon albifacies anthonyi*.
Areas 1 - 4: *Dismorphia amphiona praxinoe*; *Pereute charops charops*; *Basileuterus culicivorus culicivorus*; *Geotrygon albifacies albifacies*.
Area 5 only: *Dismorohia amphiona isolda*; *Pereute charops sphorca*; *Basileuterus culicivorus* (subsp. ?); *Geotrygon albifacies rubida*.
Area 6 only: *Dismorphia amphiona lupita*; *Pereute charops* subsp. nov.; *Basileuterus culicivorus flavescens*.

PATTERN IV

Area 1 only: *Dactylortyx thoracicus thoracicus*; *Henicorhina leucophrys mexicana*.
Area 3 only: *Dactylortyx thoracicus chiapensis*; *Henicorhina leucophrys castanea*.
Area 4 only: *Dactylortyx thoracicus fuscus*; *D. thoracicus lineolatus*; *Henicorhina leucophrys capitalis*.
Areas 5 - 6: *Dactylortyx thoracicus devius*; *Henicorhina leucophrys festiva*.

PATTERN V

Areas 1 - 4: *Mesene margaretta semiradiata*; *Dioriste tauropolis tauropolis*; *Pteronymia artena artena*; *Automolus rubiginosus rubiginosus*.
Area 5 only: *Mesene margaretta* subsp. nov.; *Dioriste tauropolis* subsp. nov.; *Pteronymia artena praedicta*; *Automolus rubiginosus guerrerensis*.

PATTERN VI

Area 1 only: *Papilio abderus abderus*; *Actinote guatemalena veraecrucis*; *Morpho achilles montezuma*; *Atlapetes brunneinucha brunneinucha*; *Chlorospingus ophthalmicus ophthalmicus*; *Cyanolyca cucullata mitrata*; *C. nana*.
Area 2 only: *Atlapetes brunneinucha apertus*; *Chlorospingus ophthalmicus wetmorei*.
Area 3 only: *Morpho achilles hyacinthus*; *Chlorospingus ophthalmicus dwighti*; *Cyanolyca cucullata guatemalae*.
Area 4 only: *Morpho achilles octavia*; *Chlorospingus ophthalmicus postocularis*; *Cyanolyca pumilo*.
Areas 3 - 4: *Papilio abderus electryon*; *Actinote guatemalena guatemalena*.
Area 5 only: *Papilio abderus baroni*; *Actinote guatemalena guerrerensis*; *Morpho achilles guerrerensis*; *Atlapetes brunneinucha suttoni*; *Chlorospingus ophthalmicus albifrons*; *Cyanolyca mirabilis*.

PATTERN VII

Areas 1 - 2: *Eupherusa eximia nelsoni*.
Area 3 only: *Eupherusa eximia eximia*.
Area 4 only: *Drucina championi championi*; *Lienix lala*; *Oxeoschistus hilarus hilarus*.

TABLE 1. Continued.

Area 5 only: *Drucina championi* subsp. nov.; *Lienix* sp. nov.; *Eupherus poliocerca*; *E. cynanophrys*.
PATTERN VIII
Area 1 only: *Prepona deiphile brooksiana*.
Area 2 only: *Prepona deiphile escalantiana*.
Area 3a only: *Prepona deiphile diaziana*.
Area 3b only: *Prepona deiphile* (subsp. ?).

In Pattern VII are included some of the most stenotopic elements of the mesophilous forest with a very restricted altitudinal distribution. These taxa have diversified into species and subspecies groups in the Mesoamerican mountains, as in the genera *Lieinix* (Lepidoptera) and *Eupherusa* (Aves).

Finally, Pattern VIII (exemplified by *Prepona deiphile*) seems to be characteristic of elements that recently arrived in Mesoamerica but have not crossed the Isthmus barrier. In this case it is not possible to generalize, since, e.g., *P. deiphile* could represent an example of rapid evolution.

In summary, we observe two kinds of endemics. First, those which have diversified subspecifically in the submontane islands of Mexico, with their closest relatives existing in the highlands of Costa Rica and Panama. These are members of polytypic species found throughout South America and Mesoamerica. These elements seem to represent the largest part of the montane hygrophilic endemics. We must note that other endemic elements have diversified in Mesoamerica and their divergence has reached higher taxonomic levels, that is, species and groups of species.

The second group agrees with Halffter's (1978) and Reyes and Halffter's (1978) ideas for the Mesoamerican Mountain Pattern; that is, they are much older groups that evolved earlier in the submontane area of Guatemala and Chiapas. It is exactly in this area that one finds the highest richness and diversity of endemics in the mesophilous montane forest.

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