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Unravelling the complexity of Mexican biogeographical patterns by naturalists in the 19th century: From Alexander von Humboldt (1769—1859) to Francis Sumichrast (1829—1882)

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Abstract

Gonzalo Halffter developed the concept of a transition zone in Mexico during the mid-twentieth century, when he superimposed the distributional patterns of different groups of Coleoptera, finding that some groups share a common biogeographical history. The complexity of the Mexican biogeographical patterns had already caught the eyes of nineteenth-century naturalists, who tried to discern some kind of order within this biotic complexity. Herein, we analyse the original studies of different nineteenth-century authors on the distributional patterns of different Mexican taxa, highlighting the main explanations provided by them. The complexity of the Mexican biota was interpreted by Humboldt as the result of the interaction between northern and southern floras, as a taxonomic peculiarity by Augustin de Candolle, as a strong biotic replacement by Alphonse de Candolle and Sumichrast, and as different dispersal stages by Wallace. Before the theory of evolution was accepted, different biogeographical patterns (endemism, diversity and taxonomic replacement gradients, among others) had coexisted without contradictions. Botanical and zoological regions first acquired a connotation of independent centres of creation, and the wider distributions (mainly disjunct distributions) later became the backbone of hypotheses concerning historical relationships between biotas based on a dispersalist model. Nevertheless, during the 20th century, the explanations of 19th century naturalists such as the limits between regions and biotic transition entered the biogeographical debate again.

Keywords: Biodiversity, biogeography, biota, dispersal, fauna, flora, transition zone

Introduction

Several authors have revisited the biogeographical patterns of the Mexican biota, mainly since the second third of the twentieth century (Smith 1941; Dice 1943; Goldman & Moore 1945; Rzedowski 1978; Morrone 2005). These studies had the shared goal of classifying the biotic identities of natural areas into a hierarchical system of provinces, dominions, regions, and realms. Their main objective was to demarcate the geographical limits of each province and to identity the species supporting them. When attempting to sort the provinces into the biogeographical regions that exist in Mexico (Nearctic and Neotropical), it was gradually acknowledged that this was not a simple task. The complexity of the Mexican biota became evident, and the existence of complex spatiotemporal patterns, with a mixed flora and fauna, was recognised. Some authors explained this complexity as the result of the superposition of different biotic histories in a common space, an idea that implies a modification of the original concept of region, which means an area that was the product of a single history shared by several taxa (Halffter & Morrone 2017).

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Other authors preferred to set the task of regionalization aside, under the premise of the existence of imbricate patterns, and focused on clarifying biotic evolutionary and biogeographical relationships. On the one hand, Léon Croizat (1958) considered southern Mexico and Mesoamerica to be one of the largest nodes ("gates") of major biotic complexity; in other words, an area where two or more biotas with independent biogeographical histories overlap. On the other hand, Gonzalo Halffter (1964, 1976, 1978) recognised a Mexican transition zone where various independent patterns overlapped, as a product of the dispersal of biotas at different moments and from different source areas. Halffter rejected the idea of the prevalence of Nearctic fauna as proposed by holarcticist theories (*e.g.*, Wallace 1876a and b; Matthew 1915) and highlighted the relevance of the patterns found in the Mexican mountains as evidence of in situ speciation events and the generation of an endemic entomofauna. The acknowledgement of Mexican biotic complexity was not an idea that emerged until the twentieth century. Alexander von Humboldt had already recognized some anomalous facts in the spatial patterns of the Mexican flora since the nineteenth century; many of his outstanding studies had undergone a series of revisions, modifications, and precisions (Juárez-Barrera *et al*. 2018). Some authors paid more attention to the existence of endemic taxa in common, while others focused more on the congruence of disjunct distributional patterns. A remarkable dichotomy between the study of biogeographical regionalization and the study of biotic evolution can be clearly appreciated since then.

Our purpose is to analyse the explanations given by some nineteenth-century naturalists for the biogeographical patterns of the Mexican biota, as well as the attempts made to rationalize their complexity. Our hypothesis is that beyond the empirical distribution data that naturalists obtained, their explanations were influenced by different theoretical principles. The main works analysed here are those of Alexander von Humboldt (1769–1859), Augustin Pyramus de Candolle (1778–1841), Alphonse P. de Candolle (1806–1893), Alfred Russel Wallace (1823–1913), Eugène Fournier (1834–1884), and Francis Sumichrast (1829–1882). Aside from any inherent historical interest that this analysis may possess, it could shed light on the debates on the regionalization and biotic evolution that are still going on today.

Humboldt: From the Andes to Anáhuac

During his trip to South America, Alexander von Humboldt started to identify some biogeographical patterns. He observed that one of the typical characteristics of tropical forests was the lack of predominant species and that the vegetation was markedly heterogeneous, unlike temperate forests, where just a few species (known as "social") dominated the physiognomy. In Mexico, Humboldt noticed some peculiarities of a vegetation type that today is known as cloud forest:

"From 17 to 22 degrees of latitude, all the country of Anáhuac, all plateau climb between 1500 to 3000 metres above the sea level is covered with oaks and a spruce species that resembles the *Pinus strobus*. Along the eastern slope mountain range, in Xalapa's valleys, a broad liquidambar forest can be found: the soil, the vegetation, and the climate also acquire the conditions of the temperate regions; a circumstance that is not observed in any other place in the meridional America." (Humboldt & Bonpland 1805: 16).

Humboldt found it difficult to regionalize the great richness and diversity of Mexican vegetation. The divisions he had recognised previously in South America, namely, warm, temperate, and cold regions, did not match up with the succession of physiognomies or their altitudinal ranges. He attempted to explain this complexity by adding the latitudinal variation to the physical conditions as a modifying factor:

"According to geodesic measures I have made in Mexico, the limit of the perpetual snows descends, in the 19th degree of boreal latitude, just at 4600 metres, 200 metres below the Equator. But in the proximity of temperate zones, the air streams that are established in the atmosphere, the direction of the trade winds, depending on which hemisphere they blow in, and other causes related to the configuration of the continents, give the regions located between 20 to 23 degrees of boreal latitude a climate and vegetation which should not be found in the tropics. Spruces of New Spain climb to 3934 metres of elevation, and even 1000 metres below perpetual snows some logs can be found, even getting as thick as 1 metre in diameter; meanwhile, between 5 and 6 latitude degrees, the tall trees disappear just at 3508 metres." (Humboldt & Bonpland 1805: 47–48).

Humboldt and Bonpland (1805) also found discrepancies in the altitudinal distribution of some species:

"Oaks (*Quercus granatensis*) do not appear in the equatorial regions, but above 1700 metres of elevation. In Mexico, between 17 and 22 latitude degrees, I have seen them descending at 800 metres." (Humboldt & Bonpland 1805: 67).

They realized another peculiarity of the Mexican vegetation, the existence of an arid plateau surrounded by mountains and covered with xeric vegetation:

"In Europe I had never observed dryness over 46 degrees. The temperature was fifteen degrees. But why, in the

Valley of Mexico, are vapours rising from the five lakes surrounding the city absorbed? Such absorption cannot be explained by the huge amounts of soda and caustic soda in the topsoil. All the inland areas of the Viceroyalty of New Spain possess an astonishing dryness. Vegetation at 2,000 metres of elevation is scarce, and the air seems to have been artificially dried, so to speak. This dryness, probably equally harmful to both health and vegetation, increases with each passing century, due to the lakes being drained by human industry and diminishing rainfall." (Humboldt & Bonpland 1805: 98).

Humboldt's observations can be summarised in three items: a) two floras converge in Mexico, a northern temperate and a southern tropical one, b) the limits between the temperate and tropical vegetation are found at higher elevations than in South American mountains, and c) the succession of plant physiognomies among the slopes in a same mountain range of Mexico consists of alternating wet and dry plant assemblages.

TABLE 1. Regions of Mexico from Alphonse de Candolle's (1855) classification.

Family	Central Mexico & Sierras		Pacific Mexico - Guayaquil		Atlantic Mexico - Guatemala	
	Species	Percent	Species	Percent	Species	Percent
Compositae	169	18.5	95	10.5	104	16
Leguminosae	66	7	125	14	42	6.5
Scrophulariaceae	43	4.5	20	2.3	40	6
Labiatae	36	4	21	2.4	33	5
Euphorbiaceae	30	4	30	3.5	17	2.6
Amentaceae	27	3			34	5
Melastomataceae			103	11.5		
Convolvulaceae			39	4.5		
Rubiaceae	19		39	4.5	21	3.2
Malvaceae			31	3.5		
Gramineae	91	10				
Orchidaceae					65	10
Total	908		883		650	

Alphonse de Candolle: One or several Mexican regions?

Mexico is one of the twenty botanical regions recognised by Augustin Pyramus de Candolle (1820). The greatest limitation of de Candolle's (1820) system was the scarce knowledge on worldwide floras and their distributional data (Juárez-Barrera *et al*. 2018). Alphonse P. de Candolle (1855) described the characteristics of Mexican flora in great detail. In contrast to the system developed by his father, Alphonse de Candolle's regionalization was not merely taxonomic or based on political frontiers (country borders), but instead demarcated the regions based on physical attributes and proposed characteristic families for each:

"Overall, from the study of the families, there are two essential characteristics to consider which can be extracted:

1. In each region, some families are dominant, speaking in terms of the proportion of their species. Such is the case of the European Gramineous and Compositae, the Leguminous in the West Indies and, in most equatorial countries the Protaces, or Myrtaces in New Netherlands, and so forth.

2. Some families are characteristic, meaning they are "dominant" to a given region, or at least they have a higher concentration of species than in other regions, sometimes compared to the phanerogams of the same region, or even compared to each family's species. Thus, Berberides are characteristic of Chile, Stilides of New Netherlands, Resedaces of the Mediterranean and its neighbouring regions, the cacti of Mexico, the oxalides of Brazil and the Cape, etc." (de Candolle 1855: 1170).

Based on this, de Candolle (1855) recognised three floristic regions for Mexico (table 1): (1) the Mexican central plateau and surrounding mountain ranges; (2) the slope from the Mexican Pacific to Guayaquil; and (3) the Atlantic slope from Mexico to Guatemala. There would be a fourth floristic region if we consider the Mexican northwest to be part of the great latitudinal desert belt (Baja California, Sonora-Arizona, Sahara and Arabia) which, along the Himalayas, according to de Candolle (1855), naturally sets apart the temperate and the tropical botanical regions in the northern hemisphere:

"This vast extension of the earth surface presents extremely different climates and, consequentially, a high diversity in the proportion of the main families. Northwards, the cold winter and the short duration of the warm season, gradually become each time more important conditions, which exclude much of the vegetation. Southwards, the drought produces a similar effect on other species. This is felt during the summer, at 45 latitude degrees in the Old World, and at 40 degrees in North America; since the duration of the drought increases toward the tropics, and the raining season is concentrated in the winter, plants suffer, unless the presence of high mountains modify such conditions. Finally, in the tropics there are regions (northwestern Mexico, Sahara, Arabia) displaying a complete drought, which determines a strong separation between equatorial regions and those of the temperate zone." (de Candolle 1855: 1241).

Thus, in the nineteenth century, both Humboldt and Alphonse de Candolle recognised various botanical regions in Mexico, which reflects their acknowledgement of the complex biogeographical configuration of the country. Alphonse de Candolle also included Mexico, along with Brazil and Cape, among the areas of greatest geographic replacement of taxa (de Candolle 1855: 1169). Alexander von Humboldt, Augustin de Candolle and Alphonse de Candolle assumed that the floras characterising each botanical region are evidence of relationship between primitive and present floras and that such ties are a result of geological history. Thereby, they shared an opposite idea to the fixism of faunas of William Swainson (1835) and Philip L. Sclater (1858).

Fournier: Widespread distribution of species patterns

After the publication of the "Origin of Species" by Darwin (1859) and its acceptance by the scientific community, Eugène Fournier was no longer particularly interested in the botanical regions, but in those species showing widespread distribution, since they supported his research into the complex relationships between the fern floras of Mexico and other areas. Fournier (1877–1879) reviewed all the collections of ferns that Alphonse de Candolle sent to him, consisting of 605 Mexican species, of which 'only' 178 were endemic (almost a third). The other 427 species were from Mexico and other countries, and most were of meridional distribution. In this group, he recognised seven distributional patterns: mountain ranges from Mexico to the Andes (230 species in the Peruvian and another 17 in the Chilean Andes); 2) Mexico and the Antilles (139 species); 3) Atlantic slope from Mexico to South America (59 reach the Orinoco river basin, 117 the Brazilian Amazon and 12 reach up to Corrientes or Montevideo); 4) temperate forests from Mexico to Chile (17, of which 11 are also found in Texas); 5) disjunct distribution in the Sierra Madre Oriental and eastern United States (Carolina to Florida), for which he did not give a number; 6) pantropical distribution (without number); and the most surprising for Fournier is group 7) with 12 species spread across the eastern slope of Mexico as far as the Mediterranean Sea (Fig. 1):

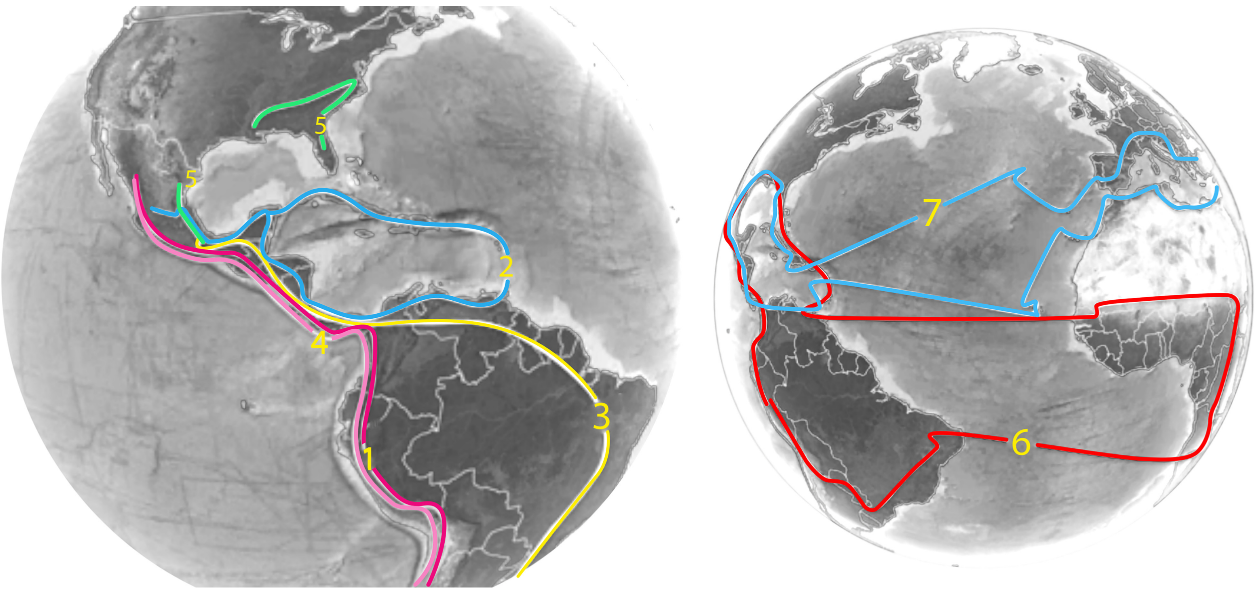

FIGURE 1. Geographical patterns of Mexican ferns (Fournier 1877–1879).

"But the most interesting plant group that concerns us is certainly, despite it being composed by no more than 12 species, that one which, throughout Gulf of Mexico slope, trespassing the Antilles, reaches the Azores and even the Canaries, ranging to the Mediterranean region, and continues with a few species in the mountains of Abyssinia, Persia or the Himalayas. Among them, *Pteris longifolia* rises toward northern mountains and stops in Eschea island, *P. creteca* in Corsica, *Woodwardia radicans* in the Asturian mountains, *Adiantum capillus* in Poitiers and Bormio, in Tyrol, near a thermal spring, *Gymnogramme leptophylla* in Brest, while *Cystopteris fragilis*, a polymorphous but indivisible species, spreads throughout all Europe and reaches the top mountains of Alpes. The authentically established existence of these plant group matches with the hypotheses sustained by several naturalists regarding the disappearance of *Atlantis*." (Fournier 1877–1879: 84).

Despite the multiple changes occurred in fern taxonomy, it is remarkable how Fournier's deconstruction of the patterns overlapping in Mexico is a similar exercise to that of Rzedowski (1991) and Halffter (1962, 1964, 1974, 1976, 1978, 1987, 2003; Halffter, Llorente-Bousquets & Morrone 2008; Halffter & Morrone 2017). Fournier supported his explanations of the continental extension hypothesis in terms of Darwin's dispersalist model (see Fichman 1977), but a very peculiar conception of evolution and the role of geological changes is evident. Fournier even invoked ideas like *Atlantis*, which represent a speculation beyond simple extensionism.

Wallace and the limits between the Nearctic and Neotropical regions

Wallace (1876a and b) adopted the system of zoogeographic regions proposed by Sclater (1858), who had already defined six primary regions based on a detailed review of the distribution of the main families and genera of birds (Wallace 1876a, Vol. I: 53). In turn, Wallace briefly summarized the current knowledge of terrestrial vertebrate distribution and explained it with reference to natural physical and biological laws (Wallace 1876a and b). Wallace applied explicitly the dispersalist model outlined by Lyell (1832) and adopted by Darwin (Wallace 1876a: vol. I: xii). He demarcated the six main zoogeographic regions, and subdivided them into sub-regions, focusing particularly on very peculiar or characteristic groups (Wallace 1876a, vol. I: 10).

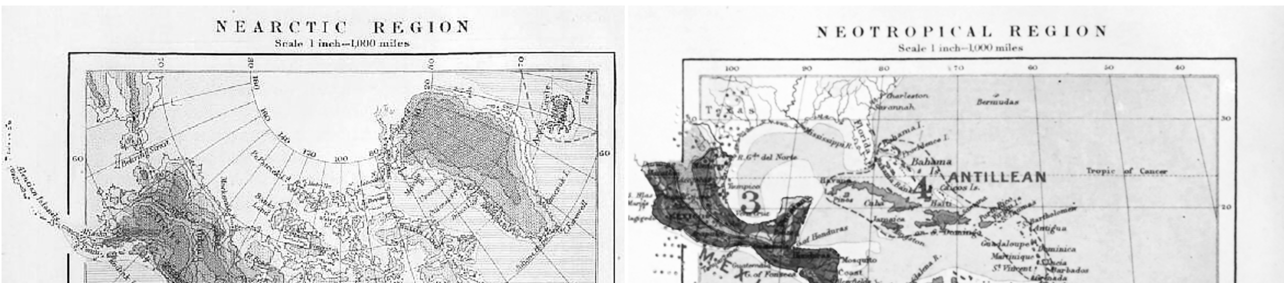

FIGURE 2. Mexico in Wallace's regions outlined in a darker shade of grey.

Wallace (1876b) included the greatest part of Mexico in the Neotropical region, together with South America and the Antilles (Fig. 2). He characterised this large region according to its enormous diversity of generic and specific forms. Due to the relative uniformity of animal life throughout the region, it was difficult for him to demarcate four sub-regions. The Antillean sub-region comprises the West Indies archipelago, characterized by its lack of diversity, which he explained as a characteristic of very old islands, but also possesses some peculiar forms that are not found in the rest of the region. The Chilean sub-region covers the temperate meridional portion of South America and the elevated Andean plateau near the Equator; its fauna is very different from that found in neighbouring tropical areas in terms of the taxa it contains and the taxa it does not. The third sub-region is Tropical South America or Brazilian sub-region, which harbours great diversity and faunistic homogeneity. Mexico and Central America, including the two slopes (Atlantic and Pacific) from the Tropic of Cancer to northwestern South America, constitute the fourth sub-region, the so-called Mexican sub-region or Tropical North America, characterized by the absence of groups that only inhabit South America (Wallace 1876b, Vol. II: 51). This sub-region possesses many genera that can be found in the Nearctic region but never in South America, and vice versa. Therefore, its fauna comprises a mixture of taxa from the north and south and Wallace, under the dispersalist model, interpreted the Mexican sub-region as possessing a fauna in a process of expansion. Wallace (1876) included all the mountain ranges surrounding the Mexican Central Plateau in the Rocky Mountains sub-region, in the southern part of the Nearctic region, which also includes the Canadian, Californian, and Alleghanian sub-regions.

Wallace (1876b) characterised the Mexican sub-region by its huge diversity of genera and species, and because of the relative uniformity of its fauna. For Wallace, it was especially difficult to demarcate this sub-region, because of the almost total absence of endemic taxa. All the genera present in the Mexican sub-region are the same as those inhabiting the Brazilian and Chilean sub-regions, each of which possess their own endemic forms. In the Mexican sub-region, some Nearctic taxa overlap with Neotropical taxa:

"The portion of North America that lies within the tropics, closely resembles the last sub-region in general zoological features. It possesses hardly any positive distinctions; but there are several of a negative character, many important groups being wholly confined to South America. On the other hand, many genera range into Mexico and Guatemala from the north, which never reach South America; so that it is convenient to separate this district as, a sub-region, which forms, to some extent, a transition to the Nearctic region." (Wallace 1876b, Vol. II: 4–5).

Wallace could not identify clear boundaries for the Mexican sub-region and considered it to be transitional to the Nearctic region. He explained this condition in terms of its recent history. Under Wallace's approach, the highlands of Mexico and Guatemala were formerly isolated from South America, forming part of the Nearctic region, which means that Neotropical elements are of recent arrival:

"Owing to the fact that the former Republic of Mexico comprised much territory that belongs to the Nearctic region, and that many Nearctic groups extend along the high-lands to the capital city of Mexico itself, and even considerably further south, there is much difficulty in determining what animals really belong to this sub-region, which forms, to some extent, a transition to the Nearctic region." (Wallace 1876b, Vol. II: 52).

Sumichrast's zoogeographic regions

Francis Sumichrast also proposed zoogeographic regions for Mexico based on those previously described by Humboldt. He divided the main physiognomic assemblages into three regions: warm, temperate, and alpine:

"From what has now been said, I infer that the department of Vera Cruz, considered as a zoological province, may be divided into three distinct regions, succeeding each other from the east to the west, and each more or less completely characterized by the predominance of certain ornithological forms peculiar to them.

The first of these regions of Vera Cruz, which, in conformity with the usual terms, I call the hot region (*terres chaudes* or *tierras calientes*), extends along the Gulf of Mexico, between the departments of Tamaulipas and Tabasco, and from the eastern border gradually rises to an altitude which we may fix approximately as about 600 metres.

The second or temperate region (*terres tempérees* or *tierras templadas*), extends from the western confines of the preceding to the foot of the Cordilleras, which form the eastern outworks of the plateau of Mexico. We assign as its limits an elevation from 600 to 1500 metres, or thereabouts.

The third, in the absence of any common term, I propose to call the alpine region, the vague name of *tierra fría*, commonly applied to the alpine region and the great central plateau to designate its climate, being inadmissible in connection with the geographical distribution of the birds. This alpine region embraces the western portions of the department, including all the mountainous portions, between 1500 and 3500 metres in height. It is quite remarkable that within a territory so circumscribed as that to which these notes are limited, we thus find, represented zoologically within a space of about 180 kilometres in breadth (taking for our line of observation the route from Vera Cruz to Mexico, and for the extreme points on this line, Vera Cruz at the sea level, and the peaks of Aculzingo, to the height of 2450 metres), the two grand natural divisions designated by naturalists under the names of Regio Nearctica and Regio

Neotropica. The union of the respective faunae of these two divisions occurs in several localities of the temperate region of the department of Vera Cruz in the most striking manner." (Sumichrast 1869: 558–559).

Sumichrast (1876) recognised a mixture of Nearctic and Neotropical faunas, but, unlike Humboldt, he also considered the existence of an endemic component, at least in the reptile fauna:

"In fact, from 54 involved genera, only seven have their highest development in the Nearctic region (*Sceloporus*, *Phrynosoma*, *Coluber*, *Bascanium*, *Eutcenia*, *Ancistroclon*, *Crotalus*), whereas at least 15 other genera (*Callichelys*, *Claudins*, *Ctenosaura*, *Phymatolepis*, *Lepidophyma*, *Heloderma*, *Loxocemus*, *Geagras*, *Stenorhina*, *Coniophanes*, *Enicognathus*, *Conophis*, *Tomodon*, *Trimorphodon*, *Symphimus*, etc.) are characteristic of the Mexican district of the Neotropical region: most of the remaining genera are essentially Neotropical." (Sumichrast 1881: 269).

He also found some species common to both the Tehuantepec Valley and Nicaragua:

"Out of the more than thirty-seven reptile and batrachian species enumerated by M. Cope, which had been collected in Nicaragua by M. Niel (Report of the Peabody Academy of Sciences 1869, p. 80), twenty-two are found to be identical over the edge of the Gulf of Tehuantepec." (Sumichrast 1881: 269).

Two ideas emerge from Sumichrast's work. First, he recognised some components endemic to the transition area, which can define it as a region with an identity of its own. Two, Sumichrast also observed that the transition between the Nearctic and Neotropical regions can be observed along an elevation gradient on the Sierra Madre Oriental in the state of Veracruz (Fig. 3).

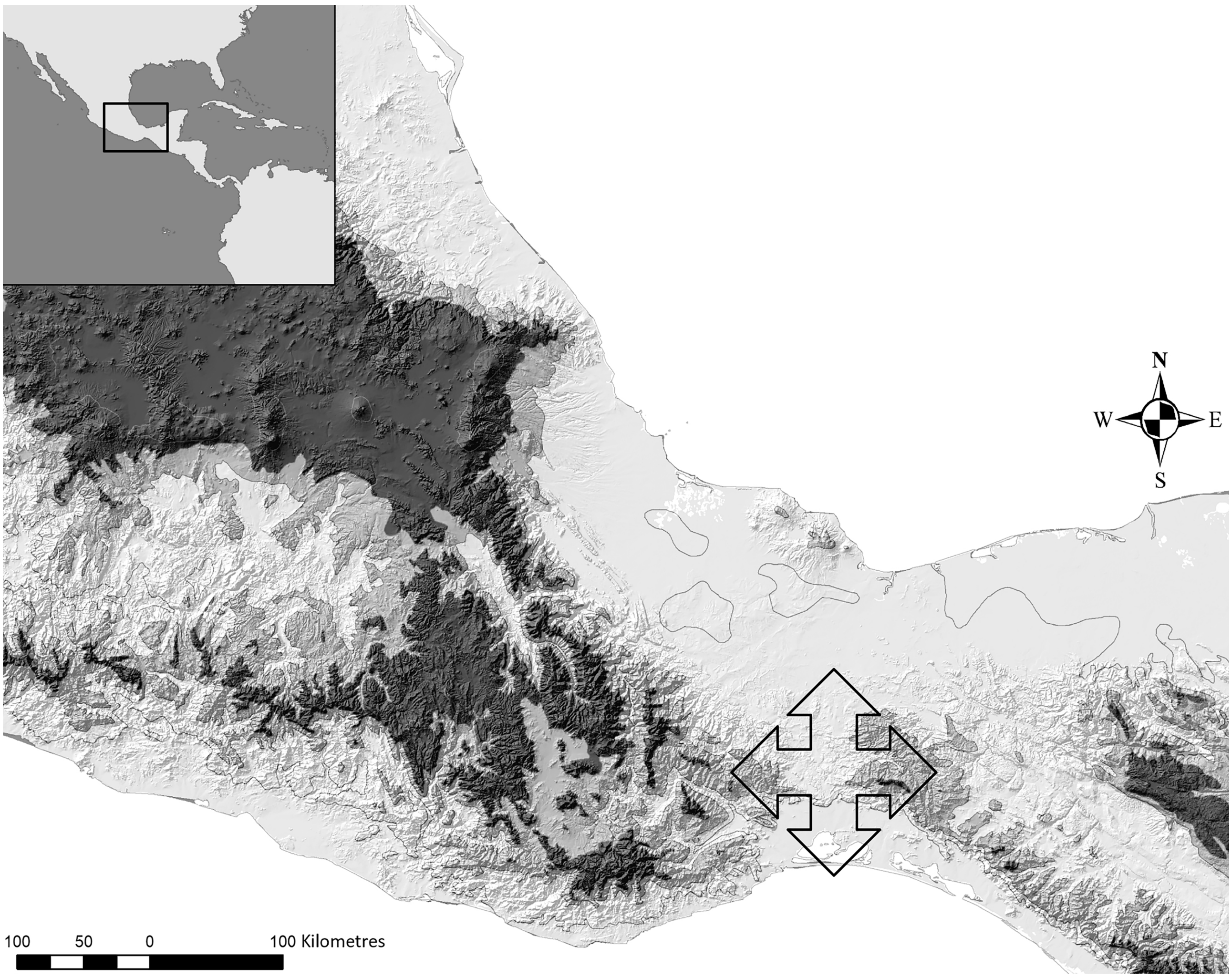

FIGURE 3. Sumichrast (1869–1881) considered the Isthmus of Tehuantepec as a transition zone both north-south and west-east.

Discussion

Humboldt's premise was that the geographical plant distribution demonstrates discrete divisions, which can be classified into regions (Ebach 2015: 26). Humboldt was interested in uncovering and understanding the complex interactions of the real world (Guarín 2004: 608). It is evident, however, that when he applied his system to the Mexican vegetation, he found several anomalies. First, the series of physiognomic assemblages are not constant in terms of their elevation or distributional patterns; second, the species diagnosed in each assemblage demonstrated hazardous distributions. Humboldt noted the necessity to fine-tune his regionalization system and to base it on distributional patterns instead of life form distribution, but he also acknowledged that the scarce taxonomic knowledge and coverage of floristic inventories were great impediments to achieve this goal.

On the Kantian premise that the world possesses an order comprising natural entities, Humboldt developed a description and classification of plant assemblages based on their physiognomy. Humboldt was not interested in the Linnaean taxonomic system to identify plant species, but rather in linking plant physiognomy to physical conditions. He tried to construct a theoretical-conceptual framework to give meaning to the huge amount of information he had compiled on plant distribution. He assumed that the geographical distribution of plants would reveal finite, discrete units that could be recognised and classified into regions. Therefore, Humboldt made an exhaustive revision of differences found in Mexican vegetation and flora. This author realised that there were differences not only between Old and New World floras, but also between those of North and South America:

"The *Cheirosthemon*, a new genus of malvaceae, about which Mr. Cervantes, a professor of Botanics in Mexico, has published an interesting monography, is found in these elevated regions; but this tree, whose flower has such a peculiar shape, has not been discovered in the Peruvian Andes." (Humboldt & Bonpland 1805: 67).

These facts led Humboldt to generalize 'Buffon's law'. Nearly sixty years before, Buffon (1776) noted that the Old and New World mammal faunas have no species in common (Nelson 1978; Kinch 1980; Larson 1986). Humboldt tested Buffon's law with plants, noticing that there were differences between the North and South American floras, and recognizing Mexico as an area where both floras overlap. Humboldt suggested characteristic taxa and boundaries between both floras:

"The vegetation of Canada and other northern regions have advanced toward south, and the volcanic mountains of Mexico are covered by the same spruces which seemed to belong only to Gila and Missouri springs." (Humboldt & Bonpland 1805: 16).

Authors such as Schouw (1823) and Grisebach (1878), among others, followed Humboldt's tradition. His ideas led to plant formation classification systems, systematic communities, and modern eco-regional systems.

Some years later, Augustin de Candolle approached plant distribution differently. He proposed a system of 20 botanical regions according to plant taxa distribution, but he warned about a lack of information. The world floras known then only represented a very small sample of estimated genera and species richness, which he calculated as a quarter (nearly 25,000 species) of his estimated total (at least 100,000). Floristic knowledge was limited by many methodological shortcomings, such as the poor taxonomic treatment of specimens and inconsistencies concerning collection or areas of distribution. That is why he considered that his system of 20 botanical regions was far from being completely developed. Mexico is one of Augustin de Candolle's 20 botanical regions, which implies that it possesses an endemic flora. Thirty-five years later, Alphonse de Candolle increased the number of botanical regions to 40 based on a better knowledge of world-flora taxonomy and the geographic evidence available. He abandoned the country-name system and demarcated more precise regions according to size and boundaries. Alphonse de Candolle highlighted 'characteristic' taxa and widely distributed species, particularly those with disjunct distribution. He discussed his ideas in his *Géographie botanique raisonnée* (Candolle 1855). In addition to other French authors like Fournier, Alphonse de Candolle explained the matching between disjunct distributions of several taxa as the product of a changing geography, implicitly accepting Edward Forbes' continental extensionist ideas. Contemporary reviews of the nature of biogeographical transition zones (i.e., Ferro & Morrone 2014) make considerations similar to those of authors such as Alphonse de Candolle, who considered deserts as zones of change between tropical and temperate regions. According to Ferro and Morrone (2014), these represent subtraction transition zones, while the mountain ranges of Mexico represent addition transition zones.

Once Darwinian theory had been accepted, interest in proposing regionalization systems gradually shifted towards the study of widely distributed taxa, which was explained in terms of dispersal from a centre of origin accompanied by differentiation events. From this point of view, congruent endemism (and even congruent disjunctions) was considered an inconsequential construct. The only tangible and undeniable pattern was the latitudinal richness gradient, which could be explained by the "general law of adaptation" (Allen 1878).

Wallace explained the geographical distribution of animals in terms of Darwin's dispersalist model, which only admits eustatic movements of sea level to connect and disconnect faunas, opposed to those hypotheses based on ancient land bridge connections. Supported by the fossil evidence, especially the unexpected discovery of several species of South American Xenarthra in North America, as well as the presence of many identical species on both sides of Central America, Wallace concluded that during the Miocene and Pliocene, North and South America had been separated by a wide sea, while the uplands of Mexico and Guatemala were connected to the North American continent at that time, which means that Mexico was originally part of the Nearctic region. Therefore, many Nearctic forms have their southern limit in Nicaragua. In the Paleogene, there were remarkable differences between the North and South American faunas. Both continents had connected only recently, producing an exchange of faunas and making it hard nowadays to set a precise boundary between the two regions. If anything, we could consider only the uplands of Mexico and Guatemala as belonging to the Nearctic region, but even today, the fauna of this area is recognised as the Mesoamerican core because of high number of endemic species. Under the dispersalist model supported by Wallace, each region may be understood to be the centre of origin of several animal lineages, but in the case of the Mexican sub-region, such an assumption is hard to support. Wallace consistently established this purpose: "… our aim is to trace the local origin or birthplace of existing genera and families" (Wallace 1876: vol. I: 108). One important problem with Wallace's proposal is that it supports the Mexican sub-region with negative characters, namely, with absences, which in contemporary biogeography equals the recognition of artificial areas of endemism, and therefore, is inadequate to properly reveal the history of the spatial distribution of taxa.

To explain the shortage of birds on the Pacific slope, Sumichrast (1881) turned to ecological explanations. For example, he argued that thrushes, which are rather typical species in temperate and cloud forests, do not exist in this area, and that other bird families which regularly eat berries are not found on the Pacific slope, where the species associated to legumes are predominant. Sumichrast observed that on the Pacific shore there is, in general, a lower diversity of birds than on the Atlantic shore, such as Sylviidae (currently the genus *Polioptila* belongs to the Polioptilidae) and Tyrannidae, specially the genus *Myarchus*. To explain the presence of birds on both shores, Sumichrast referred to the barriers (or lack of, in this case) as the cause of this faunal mixture throughout the isthmus. Sumichrast's explanation of bird distribution in the Tehuantepec Isthmus is clearly eclectic. To characterise the different areas surrounding the Isthmus of Tehuantepec, he adopted Humboldt's regions and the existence of native species, then combining physiognomy and endemism. For example, Sumichrast highlighted the existence of some characteristic reptile genera in which he called the Mexican district, which corresponds to what is now the Mexican Transition Zone. This author suggested that the transitional area between the Nearctic and Neotropical regions could be observed not only horizontally but also altitudinally. He recognized a smaller transitional zone to the one proposed by Wallace (1876b).

Sumichast's idea of considering transition areas in relation to geographical and environmental aspects is again considered in contemporary reviews (Halffter 1962, 1964, 1974, 1976, 1978, 1987; Forman 1995; Metzger & Müller 1996; Cadenasso *et al*. 2003; Fagan, Fortin & Soykan 2003; Peters *et al*. 2006; Morrone 2004). Ferro and Morrone (2014) highlight this same observation about biogeographical transition zones.

Conclusions

Humboldt explained the complexity of the Mexican biogeographical patterns by the contact between two different floras: North American and South American. In contrast, Augustin de Candolle established his Mexican botanical region because of the peculiarity of its plant families' composition, mainly cacti. Alphonse de Candolle argued that in Mexico there is a strong biotic replacement because of the existence of four botanical regions. Before the acceptance of the theory of evolution, the description of these different spatial patterns (endemism, species richness and taxonomic replacement gradients, among others) coexisted without contradictions. Each pattern implied a set of questions and explanations without excluding each other. Thereafter, the interest of some authors was focused on the study of organisms with wide distribution (mainly disjunct distributions). Hypotheses concerning the historical relationships between floras and faunas were generated based on dispersal events, since botanical and zoological regions were considered areas of creation.

Authors such as Fournier minimized the importance of endemic taxa, emphasizing the congruent distribution of widespread ferns. Based on this group, and accepting the geographical extensionist hypotheses of Forbes, Fournier proposed different relationships for Mexican pteridoflora. On the other hand, Sumichrast and Wallace adopted an intermediate position and, although they acknowledged regional limits, they explained the historical relationships between areas by dispersal events. Later, attempts at biogeographical regionalization of Mexico tried to order its complex biodiversity. In the end, the hierarchical arrangement constitutes only a preliminary framework of reference to depict a scenario where some taxa have evolved in time and space. In the 20th century, Darlington (1957) suggested the existence of a Mexican transition zone where a gradual mixture of individual distributions exists, where species showed an extension according to their dispersal capabilities. Halffter (1962 and later contributions) conceived that Mexican biota was composed of several sets of taxa historically integrated in space and time.

The contributions of 19th-century naturalists laid the foundations for the recognition of complex biogeographical patterns in Mexico. These patterns were reconsidered and analysed in the 20th century, based on a complex geography and changing environments, in the light of new evidence and analytical tools.

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