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Biogeography

Sixty years of Halffter's Mexican Transition Zone: a systematic review using bibliometric tools

Sesenta años de la Zona Mexicana de Transición de Halffter: una revisión sistemática usando herramientas bibliométricas

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Abstract

The Mexican Transition Zone (MTZ) has become a key concept that has promoted the consolidation of an integrative field of research. We reviewed the scientific publications on the MTZ with bibliometric tools to detect trends through time and analyze the conceptual structure and historiographic citation. We also performed a content analysis considering the conceptualization of the MTZ, the application of Halffter's patterns of distribution, and the different disciplines where the term has been used. The number of publications per year has not been constant, but since 2012 there has been a general increase, becoming the MTZ frequently cited in papers and in some cases constituting a research topic. We identified divergences in the conceptualization of the MTZ and discussed the implications for biogeographic studies. Halffter's conceptualization of the Mexican Transition Zone has inspired other authors to produce research focused on this area and to set biogeographic hypotheses but also to redefine the concept and make it applicable through its incorporation in the biogeographical regionalization of the Americas.

Keywords: Halffter's theory; Scientific impact; Bibliometric analysis; Content analysis; Patterns of distribution

Resumen

La Zona de Transición Mexicana (ZTM) se ha convertido en un concepto clave que ha promovido la consolidación de un campo de investigación interdisciplinario. Revisamos las publicaciones sobre la ZTM con herramientas bibliométricas para detectar las tendencias a través del tiempo y analizamos la estructura conceptual y citación historiográfica. También realizamos un análisis de contenido considerando la conceptualización de la ZTM, la aplicación de los patrones de distribución de Halffter y las diferentes disciplinas donde el término ha sido usado. El número de publicaciones por año no ha sido constante, pero desde 2012 ha habido un incremento general, llegando a ser la ZTM frecuentemente mencionada en publicaciones y en algunos casos constituyendo un tópico de investigación. Identificamos divergencias en la conceptualización de la ZTM y discutimos las implicaciones para los estudios

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biogeográficos. La conceptualización de la ZTM por Halffter ha inspirado a otros autores a producir investigación enfocada en esta área y a establecer hipótesis biogeográficas, pero también a redefinir el concepto y hacerlo aplicable a través de su incorporación en la regionalización biogeográfica de las Américas.

Palabras clave: Teoría de Halffter; Impacto científico; Análisis bibliométrico; Análisis de contenido; Patrones de distribución

Introduction

The term 'Mexican Transition Zone' has become a common, widespread concept in biogeographic studies of the Americas and Halffter's publications on the topic have been referenced in many papers and books (Halffter, 2017; Halffter & Morrone, 2017). Beyond biogeography, the term is increasingly being used in other biological areas such as systematics, ecology, and biological conservation (e.g., Joaqui et al., 2019; Lamas et al., 2014; Pinedo-Escatel et al., 2021). This evidences the role of this concept as an interdisciplinary bridge promoting the construction of an integrative field of research, helping overcome the long-established division between ecology and history, which has been an obstacle to the progress of biogeography (Crisci et al., 2003). In recent years, transition zones in other areas of the world have been increasingly analyzed (e.g., de Mendonça & Ebach, 2020; Morrone & Ebach, 2022).

Halffter referred to the Mexican Transition Zone (MTZ) in 5 contributions published in Spanish and French between 1964-1978 (Halffter, 1964, 1965, 1974, 1976, 1978). Although he clearly defined the term in some papers in Spanish (Halffter, 1964, 1965, 1976), it was in his first English paper that his definition of the MTZ became widely known as "the complex and varied area where Neotropical and Nearctic faunas overlap and that includes part of the southwestern United States, all of Mexico, and a large part of Central America extending to the Nicaraguan lowlands" (Halffter, 1987, p. 95). There were earlier mentions of the same zone by different authors who also recognized the existence of a transition between the Nearctic and Neotropical regions (e.g., Darlington, 1957; Wallace, 1876), but none of them developed a conceptual framework like that generated from the Halffter's biogeographic ideas, which has been considered as a general theory (Gutiérrez-Velázquez et al., 2013; Halffter, 2017; Morrone, 2015).

Halffter's theory is the result of the gradual development of hypotheses since 1962 to explain the distribution of the biota in the MTZ (mainly Halffter, 1962, 1964, 1987), that became a reference framework for biogeographic studies but also captured the interest of different researchers in the historical development of his proposals. Reyes-Castillo (2003) described and analyzed Halffter's contributions and showed how other researchers had previously discussed these biogeographic ideas, including some numbers about Halffter's citations at that time. Morrone (2015) presented a historiographical review of the theory, limited the MTZ strictly to the highlands of Mexico and Central America, and analyzed the biotic assemblage of different cenocrons in the transition zone. As distributional patterns, cenocrons (sets of taxa belonging to different taxonomic groups that share a geographical origin and evolutionary history and dispersed during the same time lapse) became a relevant concept in Halffter's theory. Halffter and Morrone (2017) made an analytical review describing the cenocrons and their temporal integration and reviewed the impact of the theory by describing the main biogeographic methods or subdisciplines that have been used for studying the MTZ. Other reviews (Halffter, 2017; Juárez-Barrera et al., 2020; Morrone, 2020) recognized the dynamics of Halffter's proposals in an integrative conceptual framework that explains the biotic assembly in the MTZ.

The different narrative reviews and syntheses mentioned above have summarized the contributions and highlighted the main hypotheses of Halffter's theory, allowing to promote its application in different fields and taxa; however, there are no published works that use quantifiable information to measure the impact and trends of the MTZ theory and its applicability in different biological groups and disciplines. In recent years bibliometric analyses have proved to represent replicable and objective methods (Siddaway et al., 2019), which have been applied to analyze general trends in biogeography (Morrone & Guerrero, 2008; Posadas & Donato, 2007). We use a bibliometric approach to analyze and visualize graphically the evolution and impact of Halffter's theory since 1962 and perform a content analysis considering the conceptualization of the MTZ, the application of Halffter's patterns of distribution, and the different disciplines where the concept has been used.

Materials and methods

Bibliographic search. To find all the available literature published between 1962 and June 2022, we extracted information from the Web of Science (WoS) databases using the following Boolean operator string: (ALL=(“mexican transition zone”)) OR AU=(Halffter G*) to detect occurrences of MTZ in all the fields or Halffter’s publications as some of them although referring to the MTZ were not recognized probably because they are scanned documents. This search identified 202 papers published between 1968 and 2022, and then we selected those where the MTZ is mentioned in the content and not in the titles of the references. Thus 140 documents (References in Supplementary Material) were considered and exported as a BibText file, which was then cleaned deleting duplicates and misspelled names.

Bibliometric analysis. We used the “bibliometrix” R package (Aria & Cuccurullo, 2017) for the bibliometric analysis and visualization of the results. Research trend over time was based on the number of articles published per year (annual scientific production). To explore the conceptual structure of the research on the MTZ, we used a co-word analysis to detect the inter-relationship between the most common keywords among papers and their potential grouping into clusters using a similarity measure. To analyze Halffter’s impact and detect influential articles, we performed a historiographic analysis and visualized it into a chronological citation network or historiograph, which represents the most cited references and their citation connections through time. To visualize the fifteen most cited references, authors, and keywords and their relationship, we created a three-field plot using the Biblioshiny app. Local citation refers to the number of times a reference is cited in the collection of papers analyzed.

Content analysis. To detect changes in the conceptualization of the MTZ and its main applications, we reviewed and analyzed the content of each document found by WoS to construct a database with information such as the references used to cite the MTZ, the study aim, main disciplines, biogeographic approach, biogeographic methods, Halffter’s distributional patterns (mentioned and accepted), use of the concept of the MTZ: description of distributional patterns, area delimitation (i.e., description of a study area or area of endemism), theoretical background (when used to explain or discuss results), and/or test of Halffter’s biogeographic patterns.

Results

Bibliometric analysis

General trend through time. Although the term MTZ was used in previous publications, the first detected by WoS corresponds to Halffter (1987), which was published 11 years after Halffter’s first formal definition of the MTZ

Figure 1. Number of articles per year mentioning the term Mexican Transition Zone.

(Halffter, 1976) and 25 years after his first mention of it as an overlapping area (Halffter, 1962). The use of the term was sporadic for the first years, and it was not until 1993, 6 years later, that it began to appear in indexed documents written by other authors than Halffter himself. The number of publications per year mentioning the term MTZ has not been constant, as between 1987 and 2004 there was just 1 publication per year, and then the number has been highly variable ranging from 1-18 papers/year (Fig. 1). Peaks of production occurred in 2007, 2018, and 2021. As we just included the first 6 months of 2022, it is likely to reach a higher rate of publication by the end of the year. In general, from 2012 to now there has been an increasing publication of articles using the term MTZ. It evidences that once the MTZ was widely known as a concept, it became frequently used in several papers and in some cases constituted a research topic.

Conceptual structure. The co-word analysis grouped the most frequent keywords (MTZ, biogeography, Mexico, Nearctic, Neotropics, dung beetles, panbiogeography, Trans-Mexican Volcanic Belt, etc.) into 4 clusters (Fig. 2). In each cluster, there is at least 1 biogeographic approach (phylogeography, panbiogeography, historical biogeography, and ancestral area reconstruction) and 1 biogeographic area (e.g., Trans-Mexican Volcanic Belt and Sierra Madre de Sur). In the main cluster (blue) the terms Neotropical, Nearctic, and endemism are the most closely related to the MTZ. In the second cluster (red) biogeography and Neotropics are the main nodes, related to panbiogeography and track analysis. In the third, Mexico is related to Central and North America, vicariance and historical biogeography. The last cluster (purple) shows that dung beetles (Coleoptera: Scarabaeinae) have been a focal group in the study of the MTZ.

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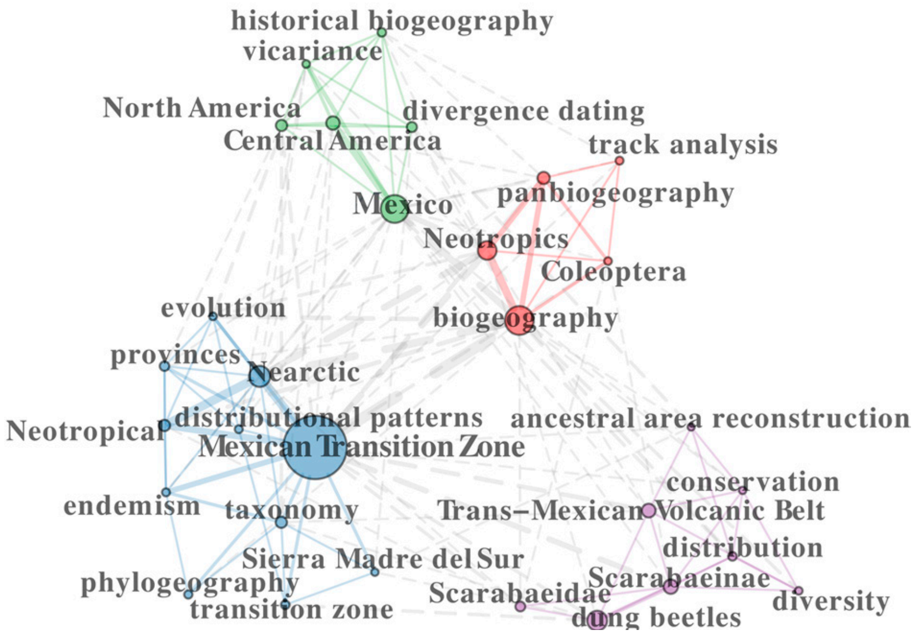

Figure 2. Keyword co-ocurrence network of the articles mentioning the MTZ.

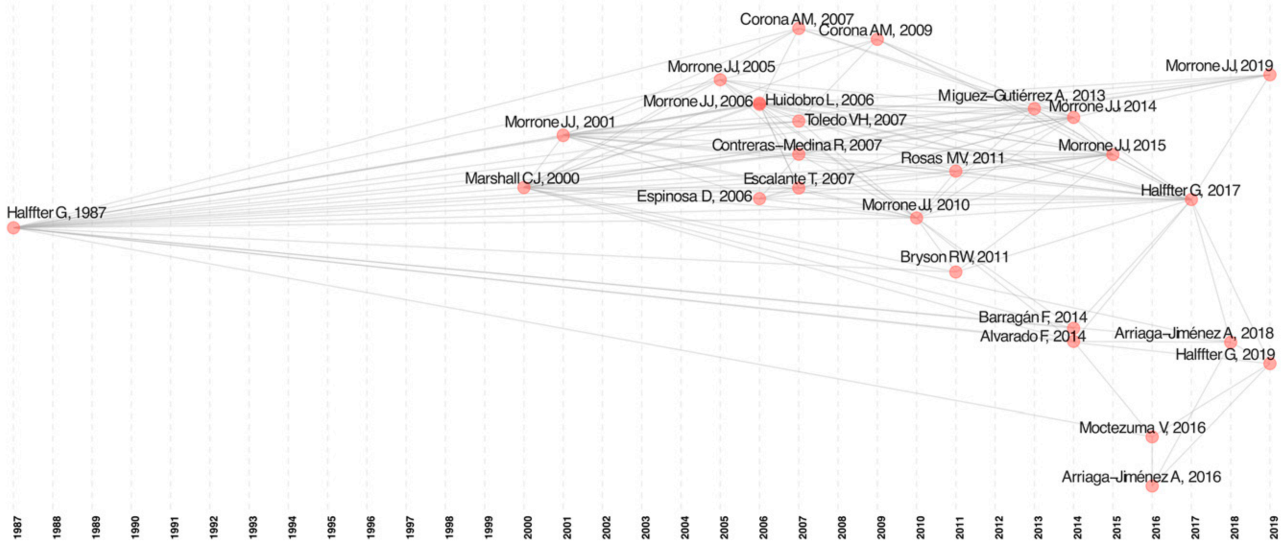

Figure 3. Historiograph of the most cited references in the local collection. Connections indicate the citation link between publications.

Impact of Halffter's contributions. The historiographic analysis detected Halffter (1987) as the most influential contribution among the papers extracted from WoS (Fig. 3). This paper was the base for the development of posterior research on the MTZ and contributed to a high inter-relationship among other researchers' contributions. If we consider the references of the papers analyzed, there are other publications such as Halffter (1964, 1976, 1978) that although not recorded in WoS, have been frequently cited and contributed to the consolidation of the MTZ as a research topic (Fig. 4). The three-field graph summarizes the fifteen most influential contributions, the authors citing them, and the main keywords used by them, which give us a general overview of the research on the MTZ (Fig. 4).

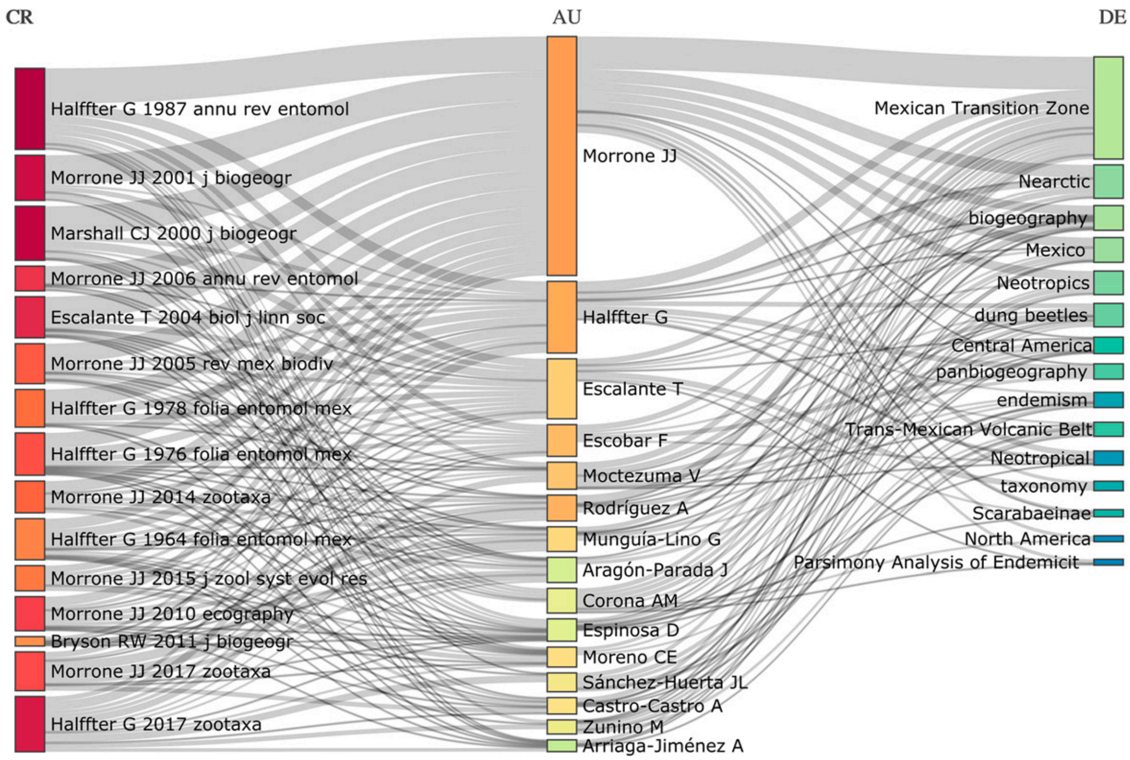

Figure 4. Three field-plot of research on the MTZ. Most local cited references (CR, left), most frequent authors (AU, middle) citing those references, and most frequent keywords (DE, right). The width of the grey connections indicates the authors' citation frequency for each reference (left) and the frequency each keyword is used by an author (right).

Content analysis

Conceptualization of the MTZ. The MTZ was conceptualized by Halffter as a transitional area occupied by biotas with Neotropical and Nearctic origins. He emphasized that it was not appropriate to delimit it geographically because biotic boundaries could depend on the analyzed group, being narrower for mammals than insects (Halffter, 1976). Among Halffter's publications on the MTZ, Halftter (1964, 1965, 1976, 1978, 1987, 2003, 2017) were papers used to reference the zone, being the most frequent those published in 1964, 1965, 1976, and 1987. Halffter (1964, p. 2) indicated that the MTZ is "the complex and varied overlapping area between Neotropical and Nearctic fauna that is located in the southern United States, Mexico, and a large part of Central America". Halffter (1965, p. 4), described the MTZ as "a wide transition zone from the Bravo River until the Chiriquí area on the border with Costa Rica and Panama". Halffter (1976, p. 5) included a detailed abstract in English where he defined the MTZ in the same way that in 1964 but added: "As a follow-up to Darlington's ideas (1957), I consider the Mexican Transition Zone…". Halffter's (1964, 1965, 1976) contributions are cited just 2 to 5 times to refer to the MTZ, while Halffter's (1987) definition published 11 years later with just minimal differences, is cited in 40 of the 139 publications found in WoS. Halffter (1976) was published in Folia Entomológica Mexicana, which is not widely available nor digitally produced. This is an example of how science communication can be affected by the language or the journals in which the ideas are published but could also be due to the more detailed definition in Halffter (1987) that includes: "…extending to the Nicaraguan lowlands". The approximate extension of the MTZ *sensu* Halffter is illustrated in Moctezuma and Halffter (2019).

Contrary to Halffter's idea of not delimiting geographically the MTZ (Halffter, 1976; Moctezuma & Halffter, 2019), Morrone (2004) restricted it to the mountain highlands based mainly on the results of a track analysis by Morrone and Márquez (2001). Morrone (2004, 2005, 2006, 2010, 2014, 2015) are the most frequently cited publications to reference the MTZ. In the first 3 publications, he considered the MTZ to have 5 provinces: Sierra Madre Oriental, Sierra Madre Occidental, Sierra

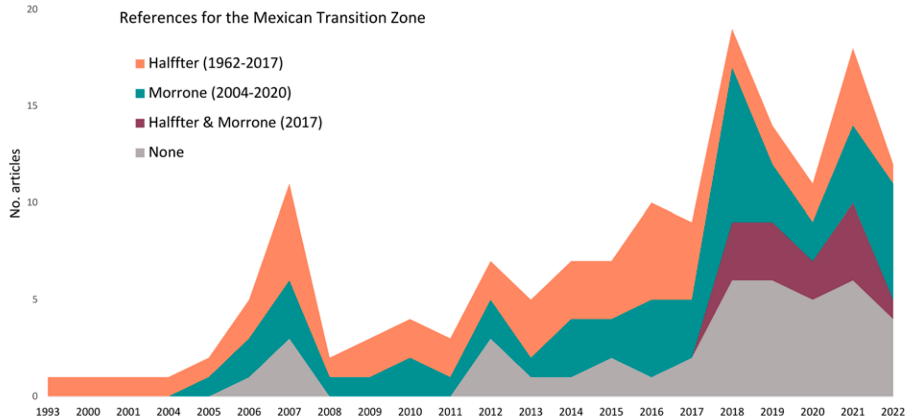

Figure 5. Number of articles using the papers by Halffter (1962, 1964, 1965, 1976, 1978, 1987, 2003, 2017), Morrone (2004, 2005, 2006, 2010, 2014, 2015, 2019, 2020), and Halffter and Morrone (2017) or none as reference to the MTZ.

Madre del Sur, Trans-Mexican Volcanic Belt, and Balsas Basin. Then, Morrone (2010) excluded the Balsas Basin, based on Espinosa et al. (2008) that considered that it belongs to the Neotropical region, and included the Chiapas Highlands as a province of the MTZ, based on Escalante et al. (2004). In posterior contributions (Morrone, 2014, 2015, 2019), the MTZ is classified both in the Nearctic and the Neotropical region with the same provinces proposed by Morrone (2010).

A large percentage of the papers analyzed use Halffter (24.5%) or Morrone (23.0%) to cite their definitions of MTZ, but most simultaneously cite both or use no reference (52.5%). In the last case, it is not possible to know what the authors mean by the MTZ, that is if they are referring to the wider extension *sensu* Halffter (1976, 1987) or if they are restricting it to the highlands of Mexico and Central America *sensu* Morrone (2014). For example, some recent papers cite Halffter and Morrone (2017), but in that review, although the authors indicated in the abstract that in a strict sense the MTZ corresponds to the mountain highlands of Mexico, Guatemala, Honduras, El Salvador, and Nicaragua, in the section "What is the Mexican Transition Zone?" they quoted the definition in Halffter (1987) without mentioning the strict sense definition. It is in the "Biogeographic regionalization" where they explained that Morrone (2005, 2006, 2014) restricted the MTZ to the highlands. So, when papers are referencing the MTZ using Halffter and Morrone (2017) it is not clear which is the concept used. There is also a small percentage of publications that uses other references for the MTZ, such as Escalante et al. (2004), and Morrone and Márquez (2001) but those also refer to the strict sense of the MTZ. The quantification of papers referencing Halffter, Morrone, and Halffter and Morrone (2017) to cite the MTZ showed that none of them has a clear tendency to increase or decrease (Fig. 5). However, the increase in the number of articles mentioning the MTZ without any reference in the last years (Fig. 5) could indicate that for some authors it has become a much more common term that does not need a specific reference.

Use of the MTZ concept. In the articles found by the bibliographic search, the term MTZ is not just mentioned but used for different purposes. In some cases, the MTZ is a core topic in the articles, and the term is used both descriptively to delimit biogeographic areas and conceptually to explain or interpret the results (Fig. 6). Most of the analyzed papers (88.5%), however, have used the term to describe the study area or to use the MTZ or some of its provinces as areas of endemism for biogeographic analyses (e.g., García-Sotelo et al., 2021; Sánchez-Chávez et al., 2019; Schramm et al., 2021). Almost half of the papers (48.2%) use the conceptual background of the MTZ to explain or discuss the results, mainly as an explanation of the high diversity and endemicity because of the mixture of biotas and geological history (e.g., Anguiano-Constante et al., 2021; Ferrari et al., 2022; Ortiz-Brunel et al., 2021; Pérez-Hernández et al., 2022) or to refer to the role of the MTZ or some of its provinces as biogeographic barriers or routes of dispersal for plants or animals (Daza et al., 2009; Gutiérrez-Rodríguez et al., 2022; Lamas et al., 2014). A little more than a quarter of the papers (25.9%) uses the MTZ theory and Halffter's patterns to describe patterns of distribution of the biological groups of interest (Arriaga-Jiménez et al., 2018; Cano et al., 2018; Joaqui et al., 2019; Rossini et al., 2018). By contrast, a low percentage of the papers (2.1%) tests biogeographic patterns or cenocrons (Corral-Rosas & Morrone, 2016; López-García & Morrone, 2022; Moctezuma et al., 2016). The low number of works testing

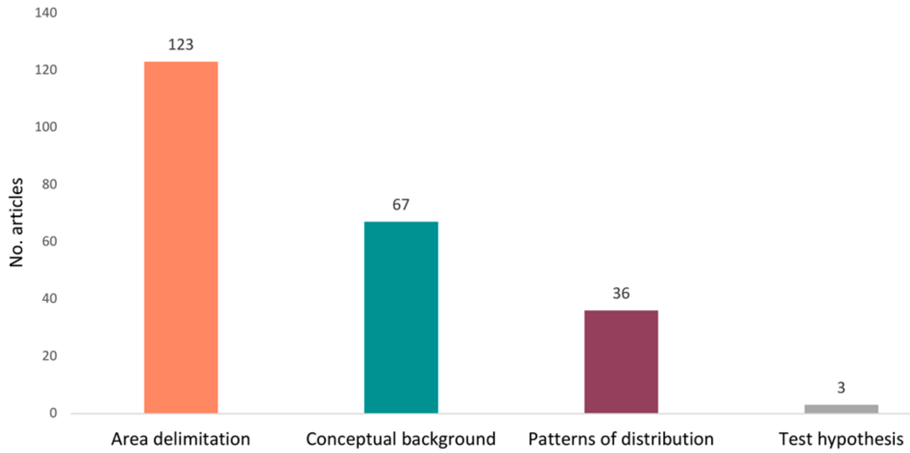

Figure 6. Number of articles using the MTZ concept for area delimitation, theoretical background, description of patterns of distribution, and test Halffter's biogeographical hypotheses.

Halffter's biogeographical patterns or cenocrons indicates that there is still a lot to explore in the application of the MTZ's theory, mainly testing its hypotheses, particularly how the geographic distribution and historical events of diversification of different biological groups could support the existence of patterns of distribution in this transition zone.

Patterns of distribution. Perhaps much more relevant than the recognition and conceptualization of MTZ was the identification and description of patterns of distribution for the biota inhabiting it, which has had significant implications for the interpretation of the biogeographical evolution of all the continent. Juárez-Barrera et al. (2021, table 2) synthesized the patterns and sub-patterns described by Halffter between 1962-2017, including their estimated age, geographic extension, and diversification in the provinces of the MTZ and continents. Halffter and Morrone (2017) explained each distributional pattern: Paleoamerican (with 5 sub-patterns), Mexican Plateau, Nearctic, Mountain Mesoamerican, and Typical Neotropical. Halffter et al. (2019) described an additional sub-pattern called Paleoamerican Mesoamerican, within the Mountain Mesoamerican pattern. Moctezuma and Halffter (2019) proposed a new pattern (Baja Californian Neotropical), and a sub-pattern (Baja Californian Paleoamerican).

Among the reviewed papers just 36% mentioned at least 1 of the patterns of distribution listed above, and 72% of them accept or support at least 1 of them from the biogeographic data for the groups analyzed. Due to its recent description and the smaller area involved, the Baja Californian Neotropical pattern is the least cited. It includes Neotropical groups such as *Canthon oblinquus*, which are endemic to the southern peninsula and that might represent an ancient migration (Miocene) to the Cape area from Sinaloa-Sonora (Moctezuma & Halffter, 2019). The remaining patterns are more frequently mentioned in different papers (20-30 articles), except the Mexican Plateau, which although being 1 of the first described (Halffter, 1962), it is just mentioned in 12 articles.

In all cases, the number of papers in which each pattern is accepted or corroborated by the group(s) is lower than the amount of papers where they are mentioned (Fig. 7). In the case of the Typical Neotropical pattern, 76.0% of the papers where the pattern is mentioned also accepted it. This youngest pattern is exemplified in the reviewed papers by South American groups that arrived to the MTZ after the Panama Isthmus closing, such as the beetle genera *Ateuchus* (Moctezuma et al., 2018), *Deltochilum*, *Dichotomius*, *Canthon*, *Eurysternus*, and *Uroxys* (Joaqui et al., 2021), *Phaneus endymion* species group (Moctezuma et al., 2019), the mammal genera *Alouatta* and *Ateles* (López-García & Morrone, 2022), and passerine birds (Ferro et al., 2017). The Mountain Mesoamerican pattern is also one of the most cited in the papers, being corroborated by taxa such as the aphodine beetle *Gonaphadiellus opisthius* (Cabrero-Sañudo et al., 2007); the weevils *Pantomorus* (Rosas et al., 2011); the bess beetles *Proculus* (Gutiérrez-Velázquez et al., 2013), *Ogyges* (Cano et al., 2018), *Chondrocephalus gemmae* and *C. granulifrons*; and the scarab *Onthophagus chiapanecus* (Pinilla-Buitrago et al., 2018). Other examples of the patterns are presented in Halffter and Morrone (2017) and Morrone (2020).

One of the main limitations of applying Halffter's patterns in particular studies could be the lack of

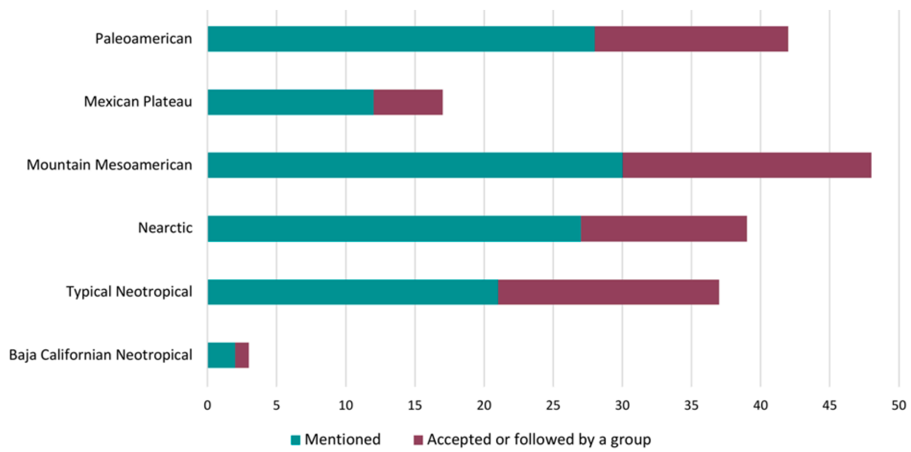

Figure 7. Number of articles where Halffter's distributional patterns are mentioned and accepted or followed by a biological group.

knowledge or proper understanding, as for many years his publications were not accessible to all researchers or scarcely divulgated. But even knowing the different described patterns and sub-patterns, selecting which is the correct for a particular group can be challenging if there is not enough knowledge on the phylogenetic relationships of the groups and about where the most closed related taxa are distributed in order to determine at least the direction of the dispersal into the MTZ. Then, estimations of the age of the biogeographic events will allow us to confirm and discriminate among patterns that are so similar in terms of current distribution. It is also likely that the classification of 1 taxon into 1 pattern changes when new evidence or data are analyzed, and even parts of that taxon can be classified into different patterns or sub-patterns as has been found, for example, in *Canthon* and *Onthophagus* (Halffter & Morrone, 2017; Halffter et al., 2019).

Disciplines and main biogeographic methods. Based on the articles found, most publications referring to the MTZ are mainly biogeographic (40.7%), systematic (18.2%), or ecological (8.7%), but the term and concept have been also applied in other disciplines such as biological conservation (1.7%) and less frequently (0.4-0.8%) agronomy, geology, archaeology, and genetics (Fig. 8A). In systematics, the MTZ has been used in taxonomic reviews and monographs for describing the distribution of the taxonomic groups studied (Falcón-Ordaz et al., 2014; Phillips-Rodríguez & Powell, 2007; Waldren et al., 2020). Most taxonomic works do not just resolve systematic problems or describe new taxa but also contribute to the knowledge of the diversity in the MTZ and offer detailed geographical information that can then be used in biogeographic analyses.

In ecological studies, richness patterns along altitudinal gradients are one of the most common topics developed and are mainly focused on dung beetles (Joaqui et al., 2021; Martín-Piera & Lobo, 1993; Salomão et al., 2021). Although, most studies have found a decrease in richness with increasing altitude, Martín-Piera and Lobo (1993) observed that the decrease is much more marked in tropical and subtropical areas than in temperate ones. Furthermore, Joaqui et al. (2021) found a mid-plateau pattern that is the result of the mixture of Nearctic and Neotropical species in the middle of the elevation gradient and highlighted the importance of considering the biogeographic affinities of the taxa analyzed when studying mountain diversity.

Among the biogeographic research, the main approaches are endemicity and track or panbiogeographic analyses (Fig. 8B). Studies analyzing diversity and/or endemism patterns were the most common, most of them Endemism Analyses using NDM/VNDM (e.g., Canales & Goyenechea, 2022; Escalante et al., 2013; Ferrari et al., 2022) but also Weighted Endemism (e.g., Anguiano-Constante et al., 2021; Ortiz-Brunel et al., 2021) was used. In most cases, these analyses using different taxa have allowed the detection of areas of the MTZ with high richness and/or endemism that could be important for biological conservation, such as the Sierra Madre del Sur for plants (Ortiz-Brunel et al., 2021) and amphibians (Canales & Goyenechea, 2022). Track analyses and Parsimony Analyses of Endemicity or PAE are more frequent (Campos-Soldini et al., 2015, Coulleri & Ferrucci, 2012; Escalante et al., 2018; Morrone & Márquez, 2001; Rosas et al., 2011; Villaseñor et al., 2020). Escalante et al. (2018) used 574 mammal species to identify generalized tracks in the Nearctic region. One of the 4 tracks was supported by Neotropical species inhabiting the MTZ, whereas the others were Nearctic tracks from the Mexican Plateau, Baja California peninsula, and the western coast

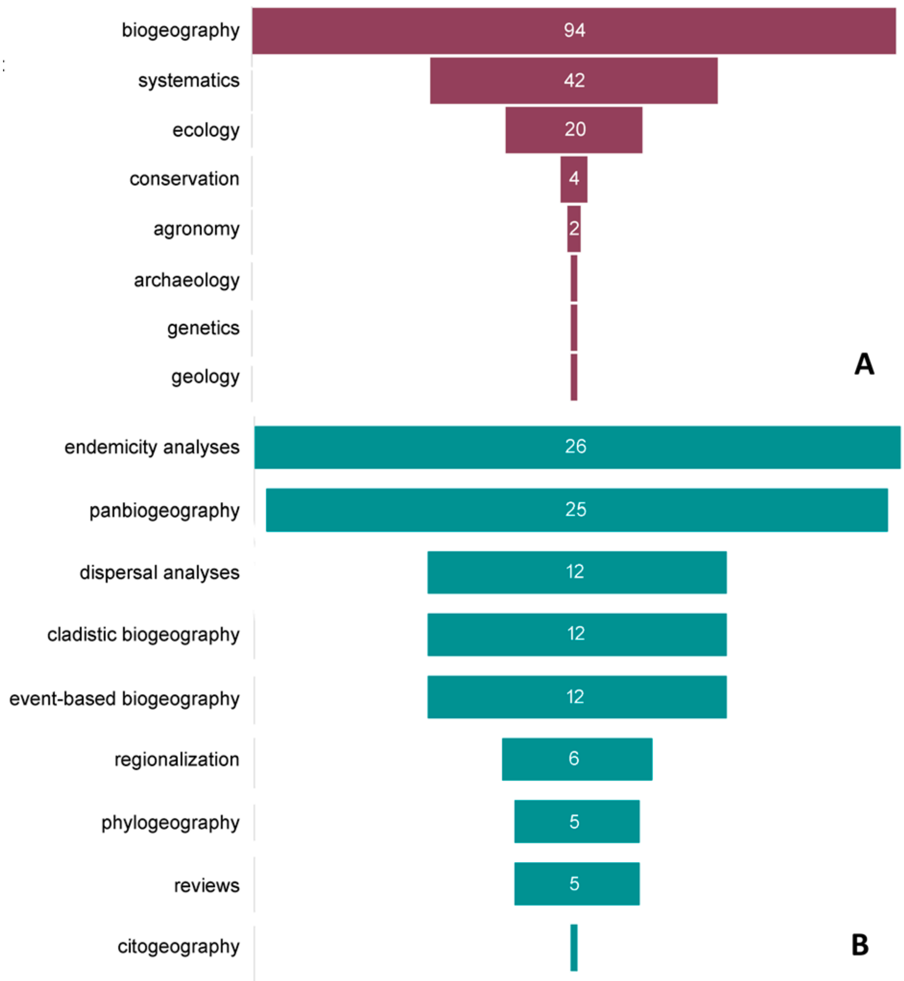

Figure 8. Number of articles where the Mexican Transition Zone is cited or mentioned by discipline (A) and main biogeographic approach (B).

of the USA. Villaseñor et al. (2020) used distributional records of 2703 genera of native plants from Mexico to determine the proportion of them characterizing the MTZ, identifying distinctive genera that define the MTZ as the mountains of Mexico from Oaxaca northwards.

Dispersal analyses, which are interpretations of the distributional patterns or try to hypothesize on scenarios of diversification were as frequent as the cladistic biogeographic studies (Álvarez et al., 2012; Cano et al., 2018; Halffter et al., 2019; Joaqui et al., 2019; Rossini et al., 2018). These analyses have contributed to the exploration of biogeographic hypotheses that imply events both of dispersal and vicariance, which can be tested with phylogenetic information and molecular dating. Most of Halffter's publications follow this approach and have been the base for the development of his main biogeographic ideas.

In cladistic biogeography, which compares the distribution and phylogenetic history of different groups to find biogeographic patterns, the most common methods applied were Brooks Parsimony Analysis (Berniker & Weirauch, 2012; Espinosa et al., 2006) and Analysis of Paralogy-free Subtrees (Contreras-Medina et al., 2007; Corral-Rosas & Morrone, 2016; Escalante et al., 2007; López-García & Morrone, 2022). One of the problems with this approach is that the conflicting results depend on the group and areas analyzed, and that cenocrons were not independently analyzed (except Corral-Rosas & Morrone, 2016). López-García and Morrone (2022) made the first cladistic analysis of the Typical Neotropical cenocron, finding a congruent pattern of area relationship due to a geodispersal event from South America after the Panama isthmus closing. Testing the remaining cenocrons would help have a better understanding of their history and diversification in the MTZ.

Almost as frequent as the cladistic biogeographic analyses were the studies classified in the so-called event-based biogeography, based on ancestral geographic range reconstruction, where Dispersal-Vicariance Analysis (DIVA or S-DIVA) (Lamas et al., 2014; Pérez-Miranda et al., 2020), Dispersal-Extinction-Cladogenesis (DEC) (García-Sotelo et al., 2021; Gutiérrez-Ortega et al., 2018) and BioGeoBEARS (Mason et al., 2018; Sánchez-Chávez et al., 2019; Schramm et al., 2021) were used to evaluate biogeographic models explaining the historical biogeography of single groups. For example, García-Sotelo et al. (2021) used the results of a phylogenetic analysis to evaluate the role of orogenic events on the diversification of *Rhadinaea* snakes. They found that the uplifting of the Trans-Mexican Volcanic Belt and Chiapan-Guatemalan highlands promoted the northward and southward colonization followed by more recent independent colonization events towards other provinces of the MTZ and the Neotropical region.

Biogeographic regionalization or area taxonomy has been another common approach where the MTZ is mentioned and analyzed (Escalante et al., 2013, 2021; Morrone, 2014, 2017, 2019; Morrone et al., 2022), which besides nomenclature area and classification, has provided maps and shapefiles. These regionalizations imply the establishment of defined limits for the MTZ which is challenging considering the transitional nature of the zone. However, they classify the biogeographic areas to provide a more practical use to the MTZ in the strict sense, being used in comparative studies that require an objective definition of areas.

Phylogeographic studies have allowed to resolve species and intraspecific limits using the obtained trees and interpret the geographic evolution of the groups in relation to geological and climatic events (Gutiérrez-Rodríguez et al., 2022; Mason et al., 2018; Schramm et al., 2021). Schramm et al. (2021) used the amblypygid species *Acanthophrynus coronatus* to test the role of vicariance and dispersal in its diversification. They found that barriers and diversification patterns were similar to other codistributed animals evidencing the impact of the Trans-Mexican Volcanic Belt orogeny and climatic changes on the Mexican Neotropical fauna. Like phylogeography but much less explored, citogeography has allowed studying the correlation between ploidy levels or chromosomic numbers and the geographic ranges of the populations. In their study of 3 species of the plant genus *Cosmos*, Castro-Castro et al. (2017) did not find an apparent correlation between the ploidy levels and geographical ranges of the species but found an increase in ploidy levels from south to north, with a concentration of polyploids in the northern Sierra Madre Occidental.

Finally, theoretical and historical reviews have been fundamental in the consolidation of the conceptual development of the MTZ (Halffter & Morrone, 2017; Juárez-Barrera et al., 2020 Morrone, 2010, 2015). Among the most recent, Halffter and Morrone (2017) presented an extensive review defining the basic terms related to the MTZ's theory, the patterns of distribution and examples of each of them with distributional maps, and the temporal integration of each pattern or cenocron into the zone. They also highlight the relevance of transition zones as valuable areas to recognize cenocrons and analyze the assembly of different biotas. De Mendonça and Ebach (2020) reviewed the 5 transition zones of the world to discuss the problems related to their biogeographic regionalization and evaluate if they were artificial or potential natural areas. They postulated that the MTZ is not a natural area but an area of biotic overlap that requires time slicing to resolve their biotic area relationships, which is the same for the South American and Indo-Malayan transition zones.

Discussion

Concluding, the main bias of the present review is that for a practical reason only the WoS platform was used and so there is a lot of information not considered in the analysis. There are also many articles that clearly focused on the MTZ but did not reference or mention the term, so the number of research focused on this topic could be clearly underestimated. The present analysis based on WoS data, however, could be replicable and constitutes an objective overview of the trends and applicability of the MTZ concept and the role of Halffter's ideas in the development of a research topic and his intellectual influence on other authors. The representative number of articles mentioning the term MTZ, which continues to increase through time, demonstrates the recognition and acceptance of the concept by different authors.

Halffter's ideas and particularly his conceptualization of the Mexican Transition Zone inspired other authors to produce research focused on this area and to set biogeographic hypotheses but also to redefine the concept and make it applicable through its incorporation in the biogeographical regionalization of the Americas. Biogeographic regionalization is a challenging task that could be also criticized because it reduces the complexity of the areas to geographic limits that are supposed to change through time. This review, however, evidenced that articles that proposed regionalizations are highly cited and used for defining endemism areas and describing distribution ranges. These regionalizations have contributed to a better understanding of the MTZ classified in both the Nearctic and Neotropical regions.

Without the incorporation of Halffter's patterns, describing the distributions of particular groups in the MTZ is reduced to being Nearctic or Neotropical, omitting the complex evolution of the biota in this hybrid zone. Halffter's ideas and their posterior development have allowed recognition that there were different moments of colonization of the MTZ that define the existence of different cenocrons. Thus, a particular biota is not Nearctic or Neotropical by the fact of being currently distributed in one of these regions, but there is a complex history of dispersal and diversification of biotas of different origins that can be explored by identifying cenocrons.

Problems with the conceptualization of the MTZ can lead to confusion and misinterpretation of published information. This review evidenced that in many cases there is no reference to the divergences in the conceptualizations of the MTZ by Halffter and Morrone, which are so different and have important implications when published information is used to delimit areas, compare, or analyze results. A possible solution could be to encourage authors to be more specific about the extension of the MTZ they are referring to and cite the correct reference in each case. A more helpful thing should be to work in the future on this conceptualization problem using distributional data and analytical tools to evaluate the advantages, viability, and applicability of both concepts to achieve consolidation.

Advances in molecular dating and the discovery and description of fossil records will give a better understanding of the approximate times when dispersal and vicariance occurred in the different lineages. For example, phylogeographic and genetic structure analyses of the dung beetle complex *Canthon cyanellus* allowed to confirm that this taxon (Nolasco-Soto et al., 2017, 2020), which was hypothesized by Halffter to be part of the Typical Neotropical cenocron, radiated during the Pleistocene, between 1.63 and 0.91 M.y.a. That likely will allow a better and easier interpretation of patterns of distribution and the application of Halffter's ideas to other taxonomic groups, including plants and other groups of animals besides insects. However, if the taxonomic and phylogenetic problems of the taxa we are studying remain unresolved or even unexplored, all efforts to advance in the study of the historic evolution and biogeography will just lead us to vague and imprecise conclusions.

Although revisions such as Reyes-Castillo (2003), Morrone (2015), Halffter and Morrone (2017), and Juárez-Barrera et al. (2020) have helped in the understanding and exemplification of the different distributional patterns, an updated review including the explanation and comparison between the most recent patterns and sub-patterns described by Halffter and his colleagues is currently lacking. This will help provide a straightforward interpretation of his ideas by other authors helping to maintain an increasing tendency in the use and application of the MTZ, contributing to a more complete knowledge about the biological diversity and biogeographic evolution of this zone.

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