

Juan J. Morrone

# The Mexican Transition Zone

A Natural Biogeographic Laboratory  
to Study Biotic Assembly

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Biotic Assembly

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*To Gonzalo Halffter,  
who taught me that biogeography is much  
more diverse and complex than I had ever  
imagined.*

*There are more things in heaven and earth,  
Horatio, than are dreamt of in our  
philosophy.  
Hamlet, act I, scene V*

*Do I contradict myself?  
Very well then I contradict myself.  
(I am large, I contain multitudes.)  
Walt Whitman (1892), Song of myself*

# Preface

I met Gonzalo Halffter twenty-one years ago. I have been invited to give a lecture on biogeography at the Instituto de Ecología, Xalapa, Veracruz. I was young (well, I thought I was young), Léon Croizat was my personal hero, panbiogeography and cladistic biogeography were the only approaches I was applying as a practicing biogeographer, and I was trying to give a good impression to my audience. After the lecture, Gonzalo asked me bluntly why I and my colleagues at UNAM considered that vicariance was the only relevant biogeographic process, dismissing dispersal at all. I felt a little uneasy, but I answered him trying to be as clear and polite as possible. After returning to Mexico City, I realized that I knew very little about Halffter's biogeographic contributions, so I decided to begin studying them. While reading them I discovered that there were other "dispersalists," like Osvaldo Reig and Jay Savage, who held ideas similar to Halffter's that both dispersal and vicariance were relevant biogeographic processes. This epiphany was surprising: these biogeographers were not the extreme dispersalists (*à la* Matthew) that I had imagined, but reasonable empirical biogeographers trying to develop an integrative approach to evolutionary biogeography.

During the following years, I had several opportunities to enjoy Gonzalo Halffter's conversation and profound knowledge. We discussed several issues, not always agreeing. My clear distinction between dispersalists and vicariance biogeographers faded away. (Conversations with Pedro Reyes Castillo and Mario Zunino were also very helpful in this respect.) Ten years ago, I developed the conviction that evolutionary biogeography was more complex than I had previously imagined, and I incorporated the dispersal–vicariance model, transition zones, and cenocrons to my perspective of biogeography. This book represents both an analysis of the Mexican Transition Zone and an empirical application of my evolutionary biogeographic perspective.

In the first chapter, I provide a general characterization of biogeographic transition zones and how they are analyzed by both the ecological and evolutionary perspectives. Several concepts are discussed and the main biogeographic transition zones of the world are briefly introduced.

In the second chapter, I present a general introduction to evolutionary biogeography, where different methods are used to answer different questions, which are considered as successive steps of an integrative analysis. I detail these steps and refer briefly to some of the methods that may be applied to answer particular biogeographic questions. I also discuss how different methods are integrated within an integrative framework, which is particularly appropriate for analyzing transition zones.

The third chapter represents a historical perspective of the Mexican Transition Zone. I refer specially to Halffter's contributions, in a historical sequence. I analyze the development of his theory and distributional patterns recognized by him, discussing how they are considered to represent cenocrons. I refer also to other authors who have analyzed the Mexican Transition Zone, undertaking dispersal, track, cladistic, endemism, and phylogeographic analyses.

In the fourth chapter, I analyze the biogeographic regionalization of the Mexican Transition Zone, characterizing its biogeographic provinces: Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, and Chiapas Highlands. I discuss their circumscription, endemic species, biotic relationships, and vegetation. I also deal briefly with the districts that have been recognized within these provinces.

The fifth chapter deals with the biotic assembly of the Mexican Transition Zone. I characterize the original Paleoamerican biota and the four cenocrons that assembled successively to it, namely, the Mexican Plateau, Mountain Mesoamerican, Nearctic, and Typical Neotropical cenocrons. I also analyze the biotic assembly of the cenocrons, from the Cretaceous to the Holocene, as well as the Paleogene, Neogene, and Quaternary horobiotas that can be recognized in the Mexican Transition Zone.

In the last chapter, I discuss some general perspectives, especially referred to transition zones and to evolutionary, ecological, and integrative biogeography. I try to analyze how integration between the historical and ecological perspectives can be undertaken in future studies.

During the years I have benefited from my interaction with several friends and colleagues, especially important for my understanding of the Mexican Transition Zone has been Gonzalo Halffter, who has generously shared his ideas with me. Pedro Reyes Castillo and Mario Zunino were also instrumental in discussing biogeographic issues. Also important have been Roxana Acosta Gutiérrez, Manuel Barrios Izás, Enio Cano, Tania Escalante, David Espinosa Organista, Ignacio Ferro, Oscar Flores Villela, Livia León Paniagua, Jorge Llorente Bousquets, Juan Márquez-Luna, Miguel Ángel Morón, Adolfo Navarro Sigüenza, Gerardo Rodríguez-Tapia, and Margarita Santiago-Alvarado. I thank them for their patience and collaboration. Federico Escobar, Juan Márquez-Luna, Gerardo Rodríguez-Tapia, and Víctor Moctezuma kindly provided photographs and maps. Adrián Fortino patiently corrected my figures and helped me improve them. Editor Lars Koerner and three anonymous reviewers provided very useful suggestions. For more than two decades, the Universidad Nacional Autónoma de México (UNAM) has generously provided me with a place to teach undergraduate and graduate students while doing research in

systematics and biogeography with the most complete academic freedom. I am indebted to Mexico, my chosen homeland, which represents so many and sometimes contradictory things that cannot be expressed appropriately with words. At home, Adrián Fortino (*Homo sapiens*), Cocoa and Gamora (*Canis familiaris*), and Emma, Tiger, Leni, and Curly (*Felis catus*) have provided love and support.

Mexico City, Mexico  
March 16, 2020

Juan J. Morrone



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# Chapter 1

## What Is a Biogeographic Transition Zone?



*Everything should be understood, and anything can be transformed—that is the modern view.*

*Susan Sontag (1992), The volcano lover*

**Abstract** A biogeographic transition zone is a geographical area of overlap, with a gradient of replacement and partial segregation between different biotas (sets of taxa sharing a similar geographic distribution as a product of a common history). It is an area where physical features and environmental conditions allow the mixture and co-occurrence of species belonging to two or more biotas, but also constrain their distribution further into one another. The biogeographic affinities of the taxa assigned to these biotas are the most fundamental information considered to analyze accurately biogeographic transition zones. Ecological biogeographers have plotted the frequency of different distribution patterns on maps, detecting gradual changes in their relative contribution to a given area and identifying the most heterogeneous places in terms of distributional patterns as transition zones. Evolutionary biogeographers have found transition zones particularly interesting for analyzing causal connections between evolutionary and geological processes at large spatial and temporal scales. Biogeographic transition zones constitute natural laboratories for investigating evolutionary and ecological principles shaping biotic assembly. Additionally, they represent places where different evolutionary lineages coexist, having important implications for conservation, particularly when they also exhibit high diversity.

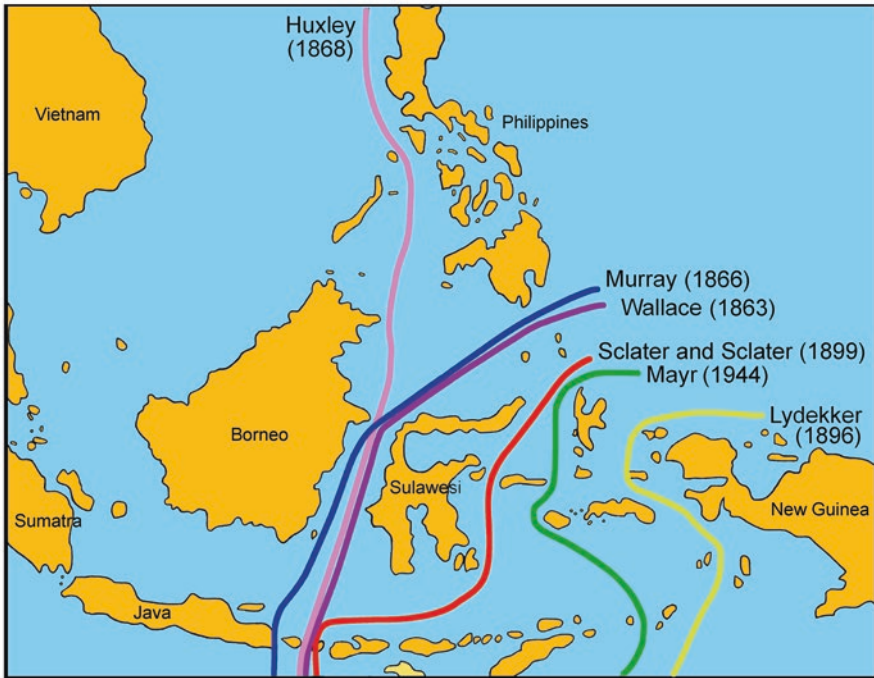
### 1.1 Introduction

The occurrence of different species and supraspecific taxa in particular geographical areas, known as Buffon's law, was noted since the eighteenth century (Morrone 2009). During the nineteenth and twentieth centuries, information on the

distributional patterns of plant and animal species accumulated, and eventually a worldwide picture emerged. The restriction of different plant and animal taxa to particular areas of the world allowed to recognize different phytogeographic, zoogeographic, and biogeographic units (e.g., Sclater 1858; Wallace 1876; Engler 1882; Takhtajan 1986; Moreira-Muñoz 2007; Holt et al. 2013; Morrone 2014a). These biogeographic units may be profitably analyzed in evolution and macroecology, to assess the degree of niche conservatism in different lineages over evolutionary time (Vilhena and Antonelli 2015).

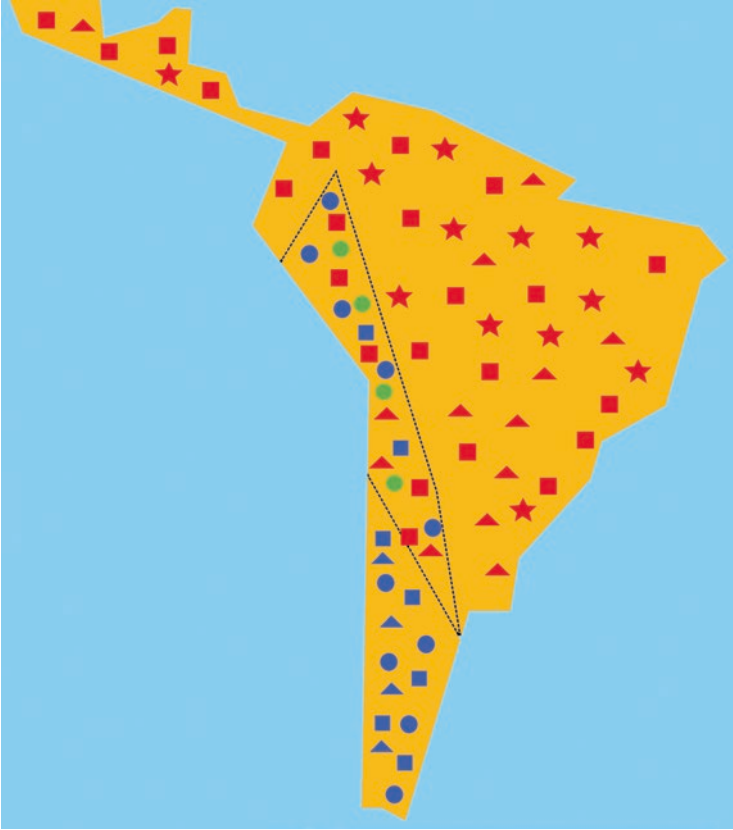
In some phytogeographic and zoogeographic regionalizations of the world, clear differences between geographically distinct biotas were noticed, and kingdoms and regions were defined, although the precise delimitation of boundaries between them was quite elusive. One of the most striking examples of the difficulties in identifying such boundaries is the archipelago that separates the Oriental and Australian biogeographic regions, in southeastern Asia. This area was studied originally by Wallace (1860, 1863), who tried to establish the boundaries separating both zoogeographic regions as a line, but found a gradual transition, with animal species of different islands showing affinities to the Oriental or the Australian region and even to India and Africa. Zoogeographers soon became aware that biotas usually intergrade into one another as zones rather than lines, but chose to represent boundaries between biotic regions using lines on maps (Ferro and Morrone 2014). The complexity of such boundaries is evidenced when comparing alternative proposals by authors studying different taxonomic groups. For example, the original “Wallace line” (Wallace 1863) was modified by Murray (1866), Huxley (1868), Lydekker (1896), Sclater and Sclater (1899), and Mayr (1944), among others, all showing different breaks in an overall transition (Fig. 1.1). (For historical accounts of Wallace’s line, see Camerini 1993 and van Oosterzee 1997.)

Biogeographic transition zones have not received the same attention than other biogeographic concepts. Although biogeographic regions and the transition zones between them are two different manifestations of the same phenomenon, the latter often remain as anecdotal within the framework of regionalization and without a parallel conceptual development (Ferro and Morrone 2014). Darlington (1957) included a section referring to transitions between regional faunas, where he stated that they are particularly complex and warned that his treatment of these zones was superficial. He defined a transition zone as the area where different faunal elements overlapped with subtractions in both directions. Pielou (1992) considered that transition zones have depauperate biotas because few elements from each region were found in the transition; however, other authors found that some transition zones may be extremely species-rich, such as the Mexican Transition Zone (Halffter 1987; Arita 1997; Ortega and Arita 1998). Morrone (2004) defined biogeographic transition zones as areas of biotic overlap (Fig. 1.2), promoted by historical and ecological changes that allow the mixture of taxa belonging to different biotas. Halffter and Morrone (2017) considered that transition zones are particularly important for evolutionary biogeography, because they allow to analyze the assembly of cenocrons with different taxonomic composition, dispersal capabilities, speciation modes, and ecological inertia.



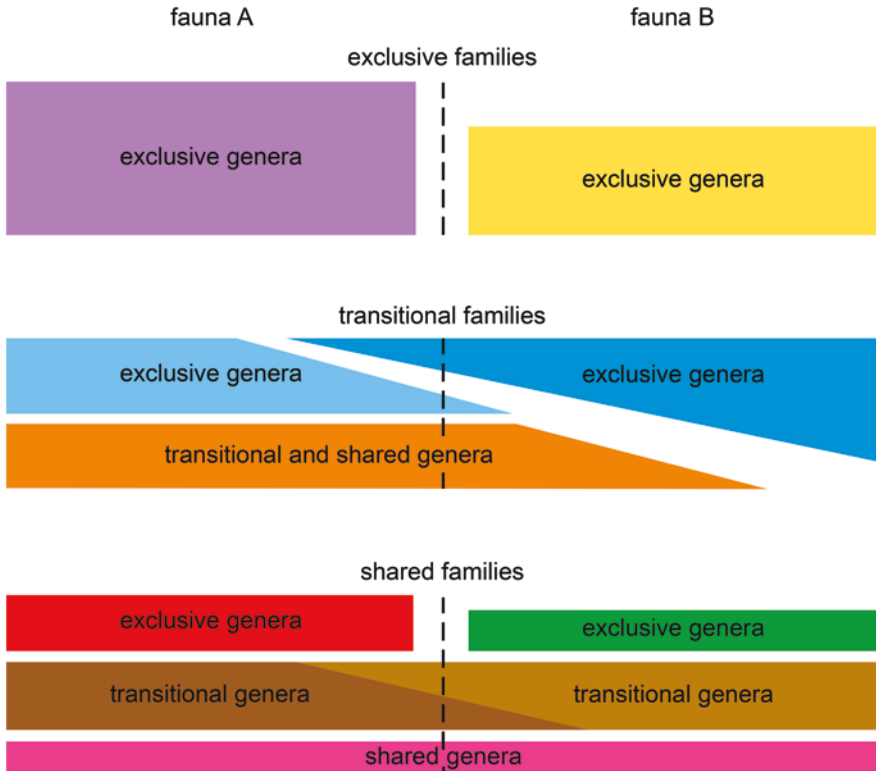
**Fig. 1.1** Delimitation of Wallace’s transition zone according to different authors

Biogeographic transition zones are specially relevant for analyzing biotic patterns and processes and to explore causal connections between biological and Earth history (Riddle and Hafner 2010). Wallace (1876) was one of the first biogeographers to realize their relevance, when acknowledging that, in addition to the overlapping distribution patterns, there were ongoing geological processes related to their development. During most of the twentieth century, authors dealing with transition zones of the world (e.g., Simpson 1940, 1965, 1977; Darlington 1957) emphasized dispersal as an explanation for the biotic assembly in the transition zone. Darlington (1957) postulated that wherever regional faunas overlap or are separated by partial barriers, a transition zone is established. Adjacent regional faunas consist of shared families, genera, and species; other taxa occur mostly in one region but extend in a part of the other; and some taxa occur in one region but not the other (Fig. 1.3). It was not until the last decades of the twentieth century (e.g., Reig 1981; Halffter 1987) that the relevance of vicariance was fully acknowledged as a contributing factor, leading to an evolutionary integrative approach (Morrone 2009). Recent advances in reconstructing Earth’s history, molecular phylogenetics, phylogeography, and lineage dating, as well as understanding the integrative nature of biogeography, have provided evidence for a more accurate characterization of transition zones and for analyzing biotic assembly (Riddle and Hafner 2010).



**Fig. 1.2** Schematic representation of the South American Transition Zone. Red symbols represent Neotropical species; blue symbols represent Andean species; green symbols represent species endemic to the transition zone

Biogeographic transition zones generally refer to boundaries between biogeographic regions, but they may exist at other hierarchical levels such as subregions, provinces, or even districts (Morrone 2006). Furthermore, there may be different types of geographical transitions (physiographic, physiognomic, climatic, etc.). The differences and similarities between the different kinds of transition zones, as well as the interaction between them, might help address the artificial distinction between evolutionary and ecological biogeography. Ferro and Morrone (2014) considered that a conceptual synthesis might be possible, by trying to discover evolutionary and ecological principles ruling biogeographic transition zones at a variety of spatial and temporal scales.



**Fig. 1.3** Schematic representation of the transition between two biotas. Each biota consists of exclusive, transitional, and shared families; and transitional and shared families consist of exclusive, transitional, and shared genera (Modified from Darlington 1957)

## 1.2 Biogeographic Transition Zones

A transition is a passage from one form, state, or place to another (Merriam-Webster 2013). Thus, a transition requires the existence of at least two different entities that are connected. Ecological transitions may be identified over a broad spectrum of spatial and temporal scales (Gosz 1993). For example, the ecotone has been defined as a transition between two or more different communities (Odum 1971) or a zone of transition between two adjacent ecological systems (Holland 1988), among other definitions. The ecotone concept arose from community ecology to indicate a change in structure and composition of plant communities, but its use was then generalized to broader spatial scales as biomes (Risser 1995) or smaller scales as patches (Gosz 1993).

The specific features of a transition zone depend on the nature of the entities between which the transition occurs; for instance, classic definitions of ecological units involve mainly functional or structural criteria (Jax 2006). In the case of

biogeographic transition zones, the involved entities are biotas, which have been considered as the basic units of evolutionary biogeography (Morrone 2009, 2014b). They are expressed graphically on maps as generalized tracks or as areas of endemism and allow the proposal of natural regionalizations (Escalante 2009; Morrone 2018). Biotas are recognized by the geographical restriction (endemism) of different plant and animal taxa to particular geographical areas. The congruence in the geographic distribution of different taxa is the product of a common evolutionary history, imposed by the vicariance of an ancient biota, which led to the independent evolution in different areas. This is the main assumption of cladistic biogeography, which postulates that the emergence of barriers isolate simultaneously the distribution of several taxa belonging to a biota producing a common history of differentiation (Morrone 2009). Thus, for a biogeographic transition zone to exist, a necessary prerequisite is the occurrence of at least two independently biotas that have evolved independently in two different areas. Eventually, barriers attenuate, and these previously isolated areas come into contact, leading to the assembly of two distinct biotas, with different biogeographic affinities and evolutionary histories. Palestini and Zunino (1986) have highlighted the relevance of the temporal dimension of transition zones, considering that their development follows three steps: transition zones appear when the possibility of biotic exchanges between two regions is established; they evolve in response to the physiographic evolution of the area, as well as the interaction of both biotas; and they may cease to exist when the barriers between the regions are re-established.

Partial barriers (Darlington 1957) or filters (Simpson 1965; Rapoport 1975) restrict differentially the distribution of each biota in the transition zone. Environmental conditions and ecological factors allow both the mixture and co-occurrence of biotas that have different geographical origins, but also constrain their distribution further one into the other. The distributional restriction of such biotas may be a strong environmental gradient of unsuitable habitats (Glor and Warren 2010). For example, sharp environmental gradients may occur in transition zones associated with mountain ranges, as the Mexican Transition Zone, where temperature variation is crucial (Antonelli 2017; Rahbek et al. 2019). Paths of unsuitable habitats may have an underlying environmental gradient but not necessarily sharp; for example, in the case of the Indo-Malayan Transition Zone, in addition to the sea arms separating different islands, there is an aridity gradient between Sundaland and the Papuan area (Mayr 1944). The Sahara Desert, which represents the transition between the Palearctic and Ethiopian (also known as Afrotropical) regions, has a gradient of aridity that seems to be a stronger barrier for passerine birds than the Mediterranean Sea (Rapoport 1975).

Whatever the kind of physical or environmental phenomena restricting species distribution of a given biota, the outcome is a more or less abrupt change in species composition of different taxonomic groups, which corresponds to a change in biogeographic affinities, in terms of present distribution and phylogenetic affinities, of the taxa involved. Partial barriers or filters do not affect exactly all species in the same way. For some species they may represent insurmountable barriers, other species may be not affected, and other species may be affected in different degrees.



Although physical and environmental phenomena restricting species distributions are prevalent all around the world, biogeographic transition zones, as considered so far only between biogeographic regions, occur in a few particular areas of the world. Therefore, there are historically contingent geological processes that are involved in the location of biogeographic transition zones (Ferro and Morrone 2014).

### 1.3 Biotas, Cenocrons, and Horobiotas

From an evolutionary perspective, it is relevant to identify biogeographic units. There are several terms that have been applied to refer to these units, namely, elements, chorotypes, areas of endemism, and generalized tracks, among others (Reig 1981; Hausdorf 2002; Morrone 2014b; Passalacqua 2015; Fattorini 2016; Ferrari 2017). When analyzing the biotic assembly in transition zones, I find useful to distinguish between two different concepts: biota and cenocron (Morrone 2009, 2014b):

A biota corresponds to the living organisms of a region (Merriam-Webster 2013). The term “fauna” may be used to refer exclusively to animal taxa and the term “flora” to refer exclusively to plant taxa. There are several concepts that may be considered related to the term “biota,” e.g., concrete biota, chronofauna, area of endemism, nuclear area, center of endemism, generalized track, biogeographic assemblage, taxonomic assemblage, and species assemblage (Morrone 2014b).

A cenocron refers to a set of taxa that share the same biogeographic history, which constitute an identifiable subset within a biota by their common biotic origin and evolutionary history (Morrone 2009). The term cenocron was proposed explicitly to refer to the dispersal and subsequent relatively synchronic implantation of a group of allochthonous taxa in a biota (Reig 1981). There are several concepts that incorporate a temporal dimension when implying the incorporation of taxa to a biota and may be considered similar to cenocron, e.g., biotic element, historical source, historical component, element, dispersal pattern, distributional pattern, lineage, and historical biota (Morrone 2014b).

Once a cenocron is incorporated to a biota, we may use the term horobiota to refer to the resulting assemblage. This term was defined by Reig (1981; as horo-fauna) as the set of species that coexist and diversify during an extended lapse and thus represent a lasting biogeographic unit. In this book I use this general term to refer to the different assemblages resulting from the dispersal of cenocrons to a transition zone (see Chap. 5).

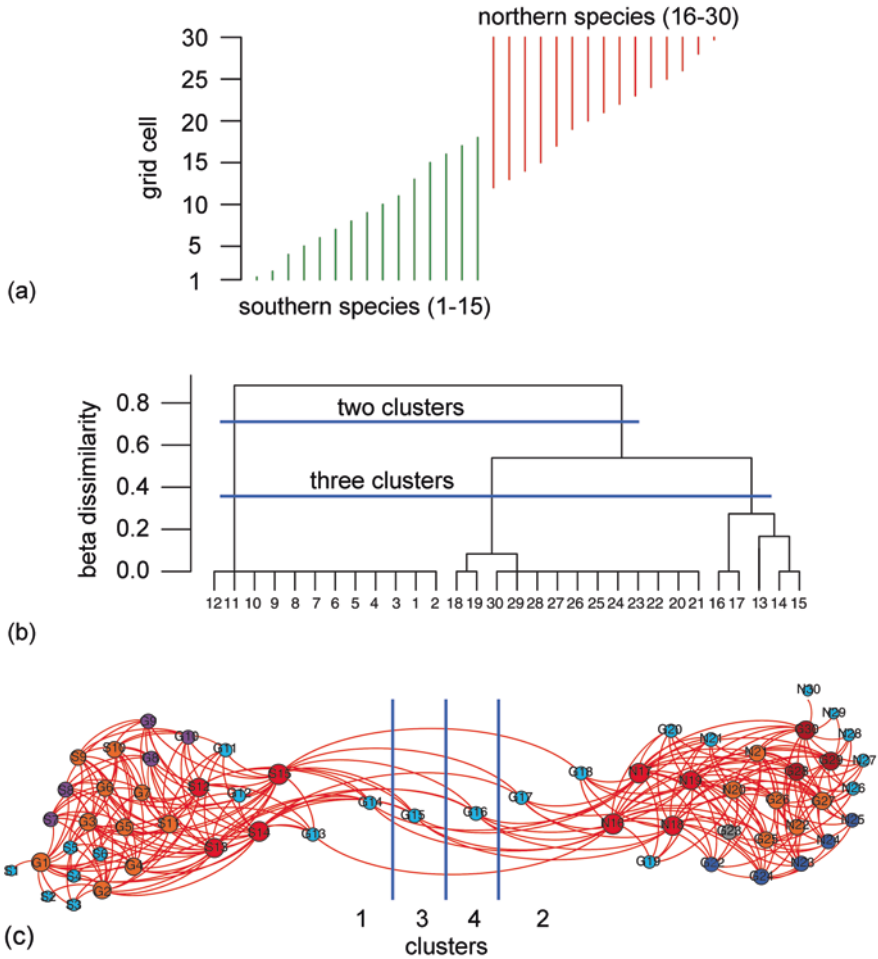
The use of these terms can allow to account for patterns resulting from both vicariance and dispersal (Morrone 2014b). Biotas are the result of vicariance, which affects several taxa at the same time, whereas cenocrons are the result of dispersal, commonly geodispersal (Morrone 2009). These terms are relative: after the assembly of a cenocron into a biota, this “new” biota or horobiota may behave in the future as a cenocron in relation to another biota. Instead of assuming dispersal or vicariance as the only driver of biotic assembly, the dispersal-vicariance model

(Brooks 2004; Lieberman 2004; Morrone 2009) considers both processes to be relevant.

## 1.4 Detection and Characterization of Transition Zones

Not all the species inhabiting a transition zone are affected exactly in the same way by partial barriers or filters. Thus, a transition zone is an area of overlap with differential penetration of taxa from one biota into another. Depending on the nature of the barrier and the taxon under study, transition zones may vary from narrow zones with strong changes in biotic composition to broad zones with gradual biotic changes along their length (Ferro and Morrone 2014). Irrespective of the nature of the barrier and considering either one taxon or the whole biota, a transition zone involves an area with a gradient of biotic change. The lines drawn on maps by early naturalists at the boundaries between major biogeographic regions are useful as easily transmissible syntheses that indicate changes in biotic composition associated with biogeographic transition zones; however, these lines fall within a zone of replacement gradients, where each author considers is located the strongest biotic interchange. Associational networks (Vilhena and Antonelli 2015) abstract species presence-absence distributional data as networks, incorporating complex relationships instead of similarity measures, where regions appear as highly interconnected groups of localities. Vilhena and Antonelli (2015) compared the performance of the species turnover and network approaches with a simulated data set (Fig. 1.4a), finding that the biogeographic transition zone may be engulfed by one of the regions when two clusters are chosen and it may represent a distinct region if three clusters are chosen (Fig. 1.4b). When they applied the network method to the same data, four clusters were found (Fig. 1.4c): one with cells 1–14, another with cells 17–30, and grid-cells 15 and 16 each forming their own clusters.

In evolutionary biogeography, transition zones may be detected by the presence of panbiogeographic nodes, namely, areas where different generalized tracks converge (Morrone 2009, 2018). These nodes point out places where biotic assembly occurs; however, they do not help distinguish the width of a transition zone (Miguel-Talonia and Escalante 2013). They are usually found in biogeographic provinces that are denoted as transitional or in the boundaries between different provinces (Escalante et al. 2004; Morrone and Márquez 2008). In cladistic biogeographic analyses, transition zones may be detected by conflicting results, where a putative transition zone may result to be the sister area to different biogeographic areas (Morrone 2009). Cladistic biogeographic analyses are based on predefined areas of endemism; thus, transition zones are represented on a general area cladogram by specific areas of endemism that have hybridized. This approach detects areas of endemism as transitional, with a defined extension and boundaries, so that the separation between the regions may be seen as a clearly defined area, in contrast with the nodes detected by track analyses. Thus, track analysis and cladistic biogeography capture different features of the transition zone (Ferro and Morrone 2014).



**Fig. 1.4** Detection of a transition zone using species turnover and network approaches. (a) Species range data across 30 grid-cells; data represent 2 biogeographic regions that overlap in a transition zone; (b) clustering these data with an unweighted pair group method, 2 or 3 clusters are obtained, where 3 clusters cause the transition zone to appear as a distinct region; (c) in the network clustering, the optimal representation is 4 clusters, where the transition zone is composed of 2 clusters, each containing a single species that cannot be confidently assigned to any of the major regions (Modified from Vilhena and Antonelli 2015)

The width of a transitional zone is variable, depending on the author's criteria. For example, Wallace (1876) considered whole subregions as transitional between biogeographic regions. Despite this, the border line of a transitional biogeographic unit assigned to a biogeographic region is usually drawn as the limit of that biogeographic region. Morrone (2006) analyzed the biogeographic regionalization of the New World and defined two groups of provinces as transitional zones between its regions: the Mexican Transition Zone between the Nearctic and Neotropical regions

and the South American Transition Zone between the Andean and Neotropical regions. The limits of these transitional provinces constitute the border of the biogeographic transition zones; however, being discrete units, these provinces cannot show the gradual change in biotic composition.

One way to characterize a biogeographic transition zone is to analyze how far “transitional” taxa are found in different areas without taking into account a biogeographic scheme other than the regional one. This approach has been used by Darlington (1957) and Simpson (1965), mainly based on qualitative descriptions of biotic overlap. Quantitative approaches used to analyze species ranges, including mapping range edge density, computing turnover rates on maps, and undertaking multivariate analyses, allow to detect changes in species composition without predefined biogeographic areas (e.g., McAllister et al. 1986; Williams 1996; Ruggiero et al. 1998; Davis et al. 1999; Williams et al. 1999; Ferro 2013). By dividing a map into equal size grid-cells and compiling the presence of species in each cell, measures of biotic similarity can be displayed on maps to visualize patterns of similarities and differentiation among groups of cells. Classification and ordination analyses, the most typically used multivariate techniques, allow to recognize and differentiate groups of cells with a similar biotic composition (e.g., Krefl and Jetz 2010). Species turnover indices directly mapped have shown to be useful to draw variations in the strength and breadth of biotic transitions, in part because they incorporate explicitly the spatial structure of the data by cell neighborhood comparison (Ruggiero et al. 1998; Williams et al. 1999).

Turnover indices can be used to break down changes in species composition across transition zones into gradients of species richness and zones of species replacement (Ferro 2013). Transition zones that exhibit an unusually high diversity may be represented by strong species richness gradients, high spatial replacement of species, or a combination of both (Ruggiero and Ezcurra 2003). The methods typically used in geographical ecology, however, treat all species as equal. To analyze thoroughly biogeographic transition zones, Ferro and Morrone (2014) considered that the gradients of biotic composition should partition the taxa analyzed into cenocrons. Thus, taxa assigned to different cenocrons should have different gradients of biotic composition.

Distributional patterns are fundamental for the analysis of biogeographic transition zones. Since shared distributional patterns are the basis of biogeographic regionalizations, the biogeographic affinities of taxa are the most fundamental information to consider in order to decompose accurately biogeographic transition zones (Ferro et al. 2017). The simplest way to define the biogeographic affinity of a given taxon is to recognize its range concordance to predefined geographical areas, such as continents in a regional-level regionalization. A more accurate way is to disaggregate range concordance according to smaller geographic areas nested within larger ones. This may generate a greater number of distributional patterns, but may allow a finer definition of their integration in a biogeographic transition zone. A quantitative approach to the definition of distributional patterns may be the identification of chorotypes, namely, the statistically significant groups of taxa with coincident distribution areas (Zunino 2005; Olivero et al. 2011; Ferro et al. 2017).