



# The spectre of biogeographical regionalization

## Abstract

A biogeographical regionalization is a hierarchical system that categorizes geographical areas in terms of their biotas. I provide a general protocol to undertake biogeographical regionalizations, that consists of seven steps: (1) defining the study area; (2) assembling distributional data; (3) identifying natural areas; (4) discovering area relationships; (5) defining boundaries/transition zones; (6) regionalization and (7) area nomenclature. Natural biogeographical units are useful for people undertaking different types of analyses, like macroecologists, evolutionary biologists, systematists and conservationists. Biogeographical regionalizations may help biogeographers communicate more effectively between themselves and discover opportunities to work on common problems, contributing to the development of a truly integrative biogeography.

## 1 | INTRODUCTION

A spectre is haunting biogeography—the spectre of biogeographical regionalization. Biogeographical regionalizations were profusely produced during the 18th and 19th centuries (Ebach, 2012, 2015; Whitaker, Riddle, Hawkins, & Ladle, 2013), but their relevance began to fade during the second part of the 20th century, with the ascent of the Modern Synthesis. One early critic, Mayr (1946), dismissed biogeographical regionalization:

*Eventually it was realized that the whole method of approach—Fragestellung—of this essentially static zoogeography was wrong. Instead of thinking of fixed regions, it is necessary to think of fluid faunas*  
(Mayr, 1946, p. 5).

Some decades later, some panbiogeographers (e.g. Craw, Grehan, & Heads, 1999; Craw & Page, 1988) felt that any attempt of regionalization is futile, because areas of endemism, which constitute the bases for regionalization, are artefactual. More recently, Cox (2001)—another dispersal biogeographer—doubted that a single biogeographical regionalization could be attainable for plant and animal taxa, and even for different animal taxa. Despite this supposed decline, biogeographical regionalizations continued being published in the 20th century, haunting their critics.

The last decades have witnessed an increasing proposition of biogeographical scenarios for particular taxa, based on molecular phylogenetic analyses and parametric event-based approaches (see review by Ronquist & Sanmartín, 2011). These analyses do not search for biotic patterns of co-occurrence among different taxa. Thus, the relevance

of biogeographical regionalizations, which are based on these patterns, could be fading again. But, paradoxically, several biogeographical regionalizations based on the analysis of large databases have been published recently (e.g. Escalante, 2017; Holt et al., 2013; Kreft & Jetz, 2010; Procheş & Ramdhani, 2012; Ribeiro et al., 2014; Rueda, Rodríguez, & Hawkins, 2013). It seems that biogeographical regionalization is back, like a spectre, haunting molecular/parametric biogeographers and others who ignore biogeographical regionalizations.

But, what is the relevance of biogeographical regionalization? Should we continue recognizing natural biogeographical areas given that molecular techniques allow to postulate complex scenarios for particular taxa? Which are the methods for discovering natural areas and detecting transition zones? How are these biogeographical areas classified? How do we name natural biotic areas? In this essay I discuss briefly these issues, reviewing the bases of biogeographical regionalization, summarizing the methods currently available and presenting a general protocol for providing natural regionalizations.

## 2 | WHAT IS BIOGEOGRAPHICAL REGIONALIZATION?

A biogeographical regionalization is a hierarchical system that categorizes geographical areas in terms of their biotas (Escalante, 2009). Biogeographical units are recognized based on distinct sets of endemic taxa and communities (Vilhena & Antonelli, 2015), representing the geographical distribution of life on Earth, modelled by past or current physical and biological forces (Kreft & Jetz, 2010).

A biogeographical regionalization is represented graphically on a map as a system of natural areas. These areas, usually recognized as areas of endemism (Morrone, 1994; Szumik & Goloboff, 2004), are based on the criterion of primary biogeographical homology, namely, area monophyly as diagnosed by different codistributed endemic species and supraspecific taxa (Ebach & Parenti, 2015; Escalante, 2009). Although some authors refer occasionally to 'phytogeographic' and 'zoogeographic' regionalizations (e.g. Cox, 2001), the ultimate goal should be to integrate all taxonomic distributions in a single biogeographical system (Morrone, 2002; Procheş & Ramdhani, 2012).

## 3 | STEPS OF A BIOGEOGRAPHICAL REGIONALIZATION

Kreft and Jetz (2010) reviewed different quantitative methods that have been used for biogeographical regionalizations, providing a



general framework to undertake them using ordination and clustering methods. I feel, however, that Kreft and Jetz's (2010) framework does not include some issues that are relevant for biogeographical regionalization, e.g. area-relationships, transition zones and area nomenclature. I present herein a modified general protocol that incorporates these issues into the general steps of a biogeographical regionalization.

### 3.1 | Defining the study area

Depending on the goal of a study, an appropriate area is selected a priori. As this step affects the following steps, it needs to be addressed adequately (Kreft & Jetz, 2010), but it is difficult to provide any advice on how to define properly the study area. If the regionalization is intended to discover natural areas within a previously recognized biogeographical scheme, it is important to include also the areas adjacent to the study area, so that the natural boundaries may be discovered. On the other hand, if we are revising or testing a previous biogeographical regionalization, we should include in the study area all the areas that have been previously considered related to the ones we are analysing.

### 3.2 | Assembling distributional data

Taxonomic distributional data from range maps, databases, monographs, systematic revisions or natural history collections constitute the bases of biogeographical regionalizations. There are basically two types of distributional data that may be used for biogeographical analyses: extent-of-occurrence maps and point information. Extent-of-occurrence maps are based on the opinion of experts and are represented on maps as polygons. Point information may be used by itself or in conjunction with distributional modelling techniques to depict distributional areas.

For most of the analyses, extent-of-occurrence maps and point information maps are superimposed to a grid. Then, grid-cells can be transferred into a presence-absence data matrix, where rows represent the grid-cells and columns represent the species. The use of grid-cells is not without problems, for example grain size may have great relevance (see Morrone & Escalante, 2002); choosing an excessively fine grain can lead to many empty grid-cells. For a world-level regionalization, Kreft and Jetz (2010) considered that a reasonable balance between accuracy and detail can be achieved using 1° or 2° latitude/longitude grid-cells, whereas Escalante (2017) detected general patterns using 4° and 8° grid-cells. Grid-cells are usually quadrangular; a recent analysis explored using hexagonal grids (Kobelkowsky-Vidrio, Ríos-Muñoz, & Navarro-Sigüenza, 2014). The problem of empty cells can be overcome by a 'moving window' strategy, as done by NDM/VNDM (Goloboff, 2011). In addition to grid-cells, there are some alternative area units that have been explored; for example latitudinal transects (García-Trejo & Navarro, 2004) or areas defined by physiographical criteria (Espinosa, Llorente, & Morrone, 2006).

Which taxa should be analysed? Although many of the first authors providing world regionalizations used supraspecific taxa

when recognizing large areas as kingdoms or regions (e.g. Engler, 1879, 1882; Wallace, 1876), it has been common in most recent studies to analyse only species. The problem with this approach is that species usually allow to discover relatively small areas (e.g. those treated as districts or provinces), so some recent authors have incorporated information on supraspecific taxa, either using phylogenetic information (e.g. Holt et al., 2013) or by considering explicitly families and genera (e.g. Escalante, 2017; Szumik & Goloboff, 2015). Procheş and Ramdhani (2012) considered that genus-level data are preferable to species- or family level data, because species-level taxonomy is often debatable and family level classification may change substantially, so genera are the best choice (see also Rueda et al., 2013). Furthermore, Procheş and Ramdhani (2012) considered that the number of genera is not so large to raise computational problems and despite differences in lineage age they can be adequate surrogates in cross-taxon analyses.

### 3.3 | Identifying natural areas

A biogeographical area is identified by the co-occurrence of two or more endemic taxa (Escalante, 2009; González-Orozco et al., 2014; Morrone, 2009). It is usually limited by geographical barriers, altitudinal ranges or a vegetation type. This distributional pattern has been considered to represent a statement of primary biogeographical homology (Morrone, 2001; Escalante, 2009), which refers to a conjecture on a common biotic history, based on the co-distributional patterns of different plant and animal taxa. Areas based on ecological grounds, known as ecoregions, may be recognized, and in occasions they can be equivalent to areas of endemism based on endemic taxa (Morrone, Escalante, & Rodríguez-Tapia, 2017). Biogeographical areas are graphical representations of biotas, which correspond to the flora (term used exclusively for plant taxa) and fauna (term used exclusively for animal taxa) of a region (Merriam-Webster, 2014), or biogeographical species pools, namely the set of species that potentially contribute individuals to a local assemblage (Carstensen, Lessard, Holt, Borregaard, & Rahbek, 2013). These biogeographical areas are commonly mapped as contiguous, in opposition to ecoregions, that are usually represented as discontinuous (Procheş, 2005).

To identify meaningful areas, and especially when dealing with large data sets, a quantitative method should be selected. There are different alternative procedures, and I will refer briefly to the most common.

#### 3.3.1 | Cluster analysis and multivariate techniques

Methods using similarity indices and clustering techniques are among the first proposed quantitative methods for delineating biogeographical regions (Carstensen et al., 2013; Kreft & Jetz, 2010; Olivero, Real, & Vargas, 1998; Procheş, 2005; Rapoport, Ezcurra, & Drausal, 1976). A variation based on the concept of adaptive affinity propagation, which allows to compute the optimal number of clusters instead of choosing it arbitrarily, was proposed by Rueda et al.

(2013) (see also Olivero et al., 1998; Olivero, Márquez, & Real, 2013). As in systematic analyses, authors should be aware that similarity does not necessarily imply naturalness, so areas identified using these methods may not represent natural areas (Escalante, 2017).

Cluster analysis may use indices of species turnover to quantify the differentiation of one region to another (González-Orozco, Lafan, Knerr, & Miller, 2013; González-Orozco et al., 2014), typically by dividing the number of shared species between two regions by some measure of the total number of species. Vilhena and Antonelli (2015) have discussed some problematic issues of species turnover.

Procheş and Ramdhani (2012) used clustering methods, but criticized that they tend to lose the connection between the areas and the taxa defining them. They considered, however, that after areas are recognized it would be possible to identify and list their endemic taxa. Vilhena and Antonelli (2015) criticized clustering methods, because they are unable to identify objectively the number of clusters that represent the data and to infer boundaries between regions.

### 3.3.2 | Parsimony analysis of endemism (PAE)

It constructs cladograms based on the parsimony analysis of presence-absence data matrices of species and supraspecific taxa (Morrone, 1994, 2014a). In contrast to other methods, PAE clearly identifies nested areas of endemism, which is useful when trying to propose a hierarchical regionalization (Escalante, 2009, 2017).

Escalante (2017) recently applied a parsimony analysis of endemism, based on mammal taxa. She found many general patterns for 4° and 8° scales, supporting some of the Wallacean regions and also adding other regions, such as the Andean region. In addition, she recovered some transition zones.

### 3.3.3 | Endemism analysis

This non-hierarchical numerical method was proposed by Szumik, Cuezco, Goloboff, and Chalup (2002) and Szumik and Goloboff (2004). It evaluates putative areas of endemism using an optimality criterion explicitly developed for endemism analyses. Endemism scores are given to the areas and higher scores indicate a stronger evidence that areas truly represent areas of endemism.

Ribeiro et al. (2014) analysed the biogeographical regionalization of the world using the grid-based method implemented in NDM/VNDM (Szumik & Goloboff, 2004; Szumik et al., 2002). Based on a data base of 4,224 species of Tipulidae (Diptera), they identified nine largest areas of endemism, which correspond to already recognized regions or subregions. They concluded, however, that the sharpness of the boundaries between traditional regions (based basically on vertebrate taxa) was unclear, due to the overlap of different biotic elements.

### 3.3.4 | Geographical interpolation

It estimates the overlap between species distributions through a kernel interpolation of centroids of the distributions and areas of

influence defined from the distance between the centroid and the farthest point of occurrence of each species (Oliveira, Brescovit, & Santos, 2015).

### 3.3.5 | Network analysis

Associational networks minimize the problems of species turnover and extract biotic association from species occurrence data (Vilhena & Antonelli, 2015). This method abstracts species distributional data as networks, incorporating complex presence-absence relationships instead of similarity measures. In the occurrence networks, regions appear as highly interconnected groups of localities. 'Infomap Bioregions' is a recently developed tool to undertake network analyses (Edler, Guedes, Zizka, Roswall, & Antonelli, 2017).

Which is the most appropriate method? There are a few analyses comparing some of these methods (e.g. Carine, Humphries, Guma, Reyes-Betancort, & Santos Guerra, 2009; Casagrande, Taher, & Szumik, 2012; Escalante, 2015), but there is no consensus on which could be the most appropriate. Fair comparisons based on large data sets should be undertaken so their similarities and differences can be assessed objectively. In some cases, empirical analyses have shown that the combination of two of these methods might be the best strategy (e.g. Escalante, Morrone, & Rodríguez-Tapia, 2013; Munguía Lino, Escalante, Morrone, & Rodríguez, 2016).

## 3.4 | Discovering area relationships

Biogeographical regionalizations have a hierarchical structure (Escalante, 2009; Vilhena & Antonelli, 2015), where smaller areas are nested within larger ones. To provide such a hierarchy, different strategies have been proposed. Olivero et al. (1998) explored the use of strong and weak boundaries for providing such hierarchy. Holt et al. (2013) considered that the incorporation of phylogenetic relationships allowed quantifying the affinities among regions more appropriately and, at the same time, to evaluate the spatial turnover in the phylogenetic composition of biotas.

The area relationships implicit in this hierarchy represent a shared biotic history (Ebach & Parenti, 2015). Monophyletic taxa are the evidence supporting biotic relationships, and allow testing biogeographical regionalizations, namely, secondary biogeographical homology (Morrone, 2001). Cladistic biogeography is the approach specifically designed to discover biotic relationships based on the phylogenetic relationships of the taxa analysed (Ebach, 2013; Morrone, 2009; Parenti & Ebach, 2009). Phylogenetic analyses for different taxa are currently being published at an extraordinary rate, so the possibilities of undertaking cladistic biogeographical analyses are enormous, although there is no agreement on which are the most appropriate methods.

## 3.5 | Defining the boundaries/transition zones

Defining boundaries between different biogeographical regions is not straightforward. Usually, different taxa show different



boundaries, so a unique 'line' cannot be drawn, but instead a 'transition zone' is represented (Morrone, 2009). Transition zones are geographical areas of overlap, with a gradient of replacement and partial segregation between different biotas (Ferro & Morrone, 2014). Whether some areas are recognized as separate regions or as transition zones may be a matter of dispute. For example Holt et al. (2013) recognized the Saharo-Arabian, Sino-Japanese and Panamanian kingdoms, but Kreft and Jetz (2013) treated them as transition zones, considering that hierarchical clustering identifies transition zones as distinct even if they result from biotic convergence rather than having an independent biotic history. When applying a cluster analysis, transition zones may be identified when regions have unstable positions between different clustering methods or different taxa (Procheş, 2005) or there are high levels of species turnover (Linder et al., 2014). Also, ordination methods may be more sensitive to distinguish core areas and transition zones, as suggested by Kreft and Jetz (2013).

Olivero et al. (2013) developed a procedure based on fuzzy sets that in addition to identifying natural areas may be used to discover transition zones. This approach assumes that boundaries between regions are usually not sharply defined but consist of broad transition zones. To avoid subjective decisions, the approach of Olivero et al. (2013) combines fuzzy logic and a statistical framework. Fuzzy logic enables to represent formally the imprecision of biogeographical boundaries, because the same area may be assigned simultaneously to different biogeographical regions or kingdoms.

Transition zones have been identified in the areas of biotic overlap of different biogeographical kingdoms or regions (e.g. Morrone, 2014b, 2015a). Their recognition at lower hierarchical levels has been suggested occasionally (e.g. Escalante, 2009; Morrone, 2006).

### 3.6 | Regionalization

To reflect the hierarchical organization of the areas recognized, a system of categories is applied. The most commonly used categories are kingdom, region, dominion, province and district (Ebach, Morrone, Parenti, & Viloria, 2008; Escalante, 2009; Morrone, 2009). If necessary, intermediate categories with the prefix 'sub' may be used, e.g. subregions, subprovinces, etc. There are other categories that have been used especially in phytosociological research, e.g. tesela, permatesela, country and sector (e.g. Rivas-Martínez, Navarro, Penas, & Costa, 2011), but their use in biogeographical regionalization has not gained support.

There is no known procedure to decide which category should be assigned to a given area, and authors have followed different strategies. Wallace (1894) discussed several principles that could be used to identify regions, namely, that they should be rich and varied in different taxa, that they should possess many peculiar taxa, and that they should lack entirely taxa abundant in other regions. Handlirsch (1913) characterized regions based on the percentage of endemic species. Udvardy (1975)

considered that kingdoms should be recognized for areas of continental or subcontinental size, with unifying geographical features. Takhtajan (1986) suggested that kingdoms should be based on endemic families, subfamilies and tribes; regions should be characterized by endemic genera; and provinces by species. Briggs and Bowen (2012) considered that provinces should possess at least a 10% of species endemism. Procheş and Ramdhani (2012) treated the clusters based on different taxa that were consistently congruent as regions, and those that were poorly defined for at least one of the taxa analysed as subregions of the region that represented the most similar cluster to them in all the analyses.

### 3.7 | Area nomenclature

Some biogeographical regionalizations (e.g. Ebach, Murphy, González-Orozco, & Miller, 2015; López, Menni, Donato, & Miquelarena, 2008; Morrone, 2014b, 2015b) have followed the nomenclatural conventions set out in the International Code of Area Nomenclature (ICAN; Ebach et al., 2008). ICAN provides a universal naming system to standardize area names used in biogeography and other disciplines, where names are grouped under more inclusive area names to represent a biogeographical hierarchy (kingdoms, regions, dominions, provinces and districts).

The notion of priority is applied to use the oldest available names instead of new names (ICAN, Art. 2.8). The work of Sclater (1858) is adopted as the date of the starting point of biogeographical nomenclature, as it constitutes the first widely adopted world biogeographical regionalization (Morrone, 2014b). In some cases widely used names were kept instead of older synonyms, applying a criterion analogous to the *nomen conservandum* convention of taxonomical nomenclature, to provide a better stability (Morrone, 2014b, 2015b).

## 4 | DISCUSSION

Whenever biogeographers communicate their ideas they need to refer to a regionalization, usually in the form of a map. Macroecologists, evolutionary biologists, systematists and conservationists, among others, also use regionalizations as general reference systems (González-Orozco et al., 2014; Holt et al., 2013; Kreft & Jetz, 2010; Vilhena & Antonelli, 2015). Biogeographical units are useful for people undertaking different types of biogeographical analyses or for communicating the results of their research to others (Morrone, 2017). For example natural biogeographical areas can be used in macroecology and evolutionary biology to assess to what extent different plant and animal species are able to cross biogeographical barriers. In addition, emphasizing the analysis of biotas rather than single taxa may have broad consequences in conservation biology (Vilhena & Antonelli, 2015). The recognition of areas of endemism in a biogeographical regionalization can be the starting point of a biogeographical atlas, which can document efficiently biodiversity

patterns in conservation biogeography (Luna-Vega, Morrone, & Escalante, 2010).

During the last decades, several authors have noted that biogeography lacks the conceptual coherence of other biological disciplines, with different approaches and methods coexisting and competing (e.g. Crisci, 2001; Ebach & Humphries, 2003; Morrone, 2009). This should not be seen as a problem, but as an opportunity for communication between different biogeographical disciplines and approaches. Biogeographical regionalizations, by their nature synthetic, may help biogeographers communicate more effectively, and when communicating between themselves, biogeographers of different viewpoints may discover opportunities to work on common problems (Morrone, 2017). Biogeographical work done on different taxa using different approaches that is synthesized into a regionalization may be profitably used as background knowledge for other studies in biogeography, ecology, biodiversity conservation and evolutionary biology.

In the 21st century, we may finally be able to fulfil the goals of the biogeographers of the previous centuries, who attempted to provide natural biogeographical regionalizations. Natural biogeographical areas have great explanatory power, because they have been moulded by common geological and biological processes (Ebach & Parenti, 2015). They may help locate observed distributional data and identify possible general patterns. When massive data contradict a regionalization, we have to question the latter and investigate what happens. Thus, regionalizations guide the identification of patterns and, at the same time, change with incongruent distributions or with newly identified patterns. The massive incorporation of molecular phylogenetic analyses will undoubtedly have a huge impact in biogeography, with possibilities of testing and refining the available regionalizations, as well as proposing new ones, although the perils of building a narrower research program are worrying (for a similar situation in systematics see Crisci, 2006). In addition, natural biogeographical areas may coincide with ecoregions based on climatic, geological and biotic criteria (Morrone et al., 2017), allowing to synthesize biotic and abiotic information in an efficient way, and providing links between evolutionary and ecological biogeography. Instead of haunting modern molecular/parametric biogeographers, I hope biogeographical regionalizations become instruments for a comprehensive rethinking of biogeographical concepts and help develop a truly integrative biogeography.

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