

# The dichotomy of the modern bioregionalization revival

Malte C. Ebach<sup>1\*</sup> and Lynne R. Parenti<sup>2</sup>



<sup>1</sup>School of Biological, Earth and Environmental Sciences, UNSW, Sydney, NSW 2052, Australia, <sup>2</sup>Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

## ABSTRACT

The modern bioregionalization revival is marked by an abundance of revised biogeographical classifications along with new analyses at both local and global scales. Many of these new regionalizations are based on sophisticated geospatial and species distributional models whereas others focus on the information about area relationships as inferred from the phylogenetic relationships of taxa in the areas. This results in a dichotomy between geospatial and phylogenetic approaches: areas may have the same name, but different composition and relationships. We see an opportunity to move bioregionalizations forward by proposing new regions or revising well-known regions to reflect the advances that have been made in our understanding of phylogeny, biodiversity and Earth history during the past 50 years. Twenty-first century biogeographers can adopt the methods of phylogenetic systematics which prescribe how taxa and their characters may be used to infer hierarchical relationships. In an analogous way, natural bioregions may be discovered by treating biotic areas as taxa and finding aggregate patterns of distributional relationships – a general areagram – as specified by phylogenies of the clades that live in those areas. We demonstrate the differences in these two approaches – general areagrams versus distributional models – in bioregionalizations and definitions of the Australian and the Neotropical regions.

## Keywords

Australia, area monophyly, comparative biogeography, discovery, Eremaean, general areagrams, historical biogeography, Neotropical region.

\*Correspondence: Malte C. Ebach, School of Biological, Earth and Environmental Sciences, UNSW Australia, Sydney, NSW 2052, Australia.  
E-mail: mcebach@unsw.edu.au

## INTRODUCTION

To search for natural biogeographical areas is a centuries-old obsession of plant and animal geographers. How best to name the natural regions of the world has been debated at least since 1777 when E.A.W. von Zimmermann first proposed global animal regions. Are there naturally a New World and an Old World? What proportion of plants and animals do they share? Should smaller regions be grouped into larger regions? The modern era of biogeography was spurred on by Alfred Russel Wallace's hypothesis (letter to H.W. Bates, January 4, 1858, in Marchant, 1916) that the western part of the Malay Archipelago was '... a separated portion of continental Asia while the eastern part is a fragmentary prolongation of a former west Pacific continent'. Two modern biogeographical principles – endemism and terrane fidelity – came together to bolster Wallace's theory of organic evolution and to illustrate the intimate connection

between the biotic and abiotic world. Subsequently, Wallace (1876) adopted the continent-based classification of global zoogeographical regions (Palearctic, Ethiopian, Oriental, Australian, Neotropical and Nearctic) proposed by ornithologist Philip L. Sclater (1858). Continent-based classifications were thought to better reflect natural area relationships and geology than did classifications based on, for example, latitudinal gradients that followed isotherms (e.g. Forbes, 1854). Yet this classification is silent on relationships among the continents and their biota.

Modern biogeographers are so familiar with the Sclater–Wallace regions that many would be surprised to know that the original proposal of the regions sparked a fierce debate. Wallace's zoogeographical classification was popular, but many of his contemporaries thought his areas too precise. Others rejected area hierarchy, arguing that smaller, familiar life-zones should be independent of larger, more abstract regions. By the end of the 19th century, the debate surrounding regions

and regionalizations had subsided (Whittaker *et al.*, 2013). Bioregionalizations are back in full force (Table 1). The desire and need to recognize and name natural areas is as great today as it was 150 years ago. A new debate has arisen: are these areas natural entities or just artefacts, human constructs? And how may we recognize the difference?

We review the 19th century biogeographical debate about area descriptions to show that it is fundamentally the same as modern debates about regionalizations and thus reinforces the need for an empirical method to discover and test natural areas. We then review a methodological protocol to discover natural regions and demonstrate how it alters our understanding of the biogeography of Australia and what we call the Neotropical region.

### THE 19TH CENTURY DEBATE: DESCRIBING THE NEARCTIC, PALAEARCTIC AND HOLARCTIC AREAS

Between 1882 and 1883, a debate erupted in Europe and North America over the proposal to merge two widely adopted Sclater–Wallace zoogeographical regions, the Nearctic and Palaeartic, into a single region, the Holarctic. Naturalist Angelo Heilprin (1882, p. 316) declared the Nearctic ‘...so directly contradictory that a reconsideration is rendered almost imperative’. Wallace thought Heilprin’s objections unwarranted, arguing that if the search for ‘these well-marked and most natural primary divisions’ was abandoned, it ‘...would open up questions as regards the remaining regions which it will not be easy to rest’ (Wallace, 1883, p. 483). Continuing his objections, Heilprin (1883, p. 605, original italics) insisted that ‘...a marked absence of *positive* distinguishing characters’ does not justify description of a region. After all, the Nearctic and Palaeartic *share* many mammalian taxa. The absence of distinct European plants and animals from North America was no reason to recognize it as a region.

The dispute would not end. American ichthyologist Theodore Gill concluded that:

The facts of zoogeography are so involved, and often apparently contradictory, that a skilful dialectician with the requisite knowl-

edge can make plausible argument for antithetical postulates. Prof. Heilprin, being a skilful dialectician and well informed, has submitted a pretty argument in favour of the union of the North American or ‘Nearctic’ and Eurasiatic or ‘Palaeartic’.

(Gill, 1883, p. 124)

No real consensus or evidence emerged (Ebach, 2015). Allen, like Gill, saw this incessant splitting and lumping as sophistry or an easy way out:

These divisions, as has been urged recently in the favour [by Wallace (1876)], are *convenient and easy to remember*, since they are approximately equal in size, are easily defined, and avoid complicated boundaries.

(Allen, 1892, pp. 211–212, italics in original)

By the early 20th century, regionalizations had stalled. Old regions were redescribed rather than new regions discovered. By the 1940s, various regionalizations were in use, none of which was tested for natural divisions. Many zoogeographers were unsure about the degree to which regions were arbitrary, ironically leading to the tacit acceptance of the arbitrary nature of zoogeographical regions: ‘It may prove impossible to devise a system equally well suited to the diverse needs of workers in widely separated fields of biology, but agreement upon at least the major units in biogeographic classification is desirable’ (Dice, 1943, p. 7). Lee R. Dice was ready to negotiate. But, the engineers of the newly emerging Modern Synthesis were quick to dismiss regionalization:

Eventually it was realized that the whole method of approach – *Fragestellung* [question] – 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)

This reflected the concurrent rejection of classification by ecologists:

To call ecology a classifying science may seem a stretch, because it clearly is not one at present. But it was in its formative decades, from the 1890s until about 1940, when ecologists (at least in the United States) disavowed this aspect of their history as a false start. Classifying as an end in itself came to stand for all the shortcomings of a ‘merely’ descriptive science before it became properly analytical and causal.

(Kohler, 2008, p. 80).

Of course, the things ecologists were classifying – groups of species in, for example, a grassland – did not necessarily share a history, so classification in ecology and classification in botany and zoology had different goals. Nonetheless, we demonstrate below that biogeographical classifications of bioregionalizations that incorporate information on relationships among areas are analytical, not just descriptive (*sensu* Ball, 1976).

### THE 21ST CENTURY: THE BIOREGIONALIZATION REVIVAL

The current bioregionalization revival, encouraged by the availability of massive amounts of data and an equal amount of processing power, has resulted in an abundance of large-scale analyses (Table 1; see Kreft & Jetz, 2010). Most of these

**Table 1** Representative recent large-scale bioregionalizations

Area	Reference
Neotropical region	Morrone (2014a,b)
Australia	Ebach <i>et al.</i> (2013)
Terrestrial zoogeographic regions	Holt <i>et al.</i> (2013)
Terrestrial zoogeographic regions	Rueda <i>et al.</i> (2013)
Nearctic	Escalante <i>et al.</i> (2013)
Sub-Saharan Africa	Linder <i>et al.</i> (2012)
Southern Ocean	Rogers <i>et al.</i> (2012)
Marine provinces	Briggs & Bowen (2012)
Antarctic	Terauds <i>et al.</i> (2012)
Austral floristic realm	Moreira-Muñoz (2007)
Marine ecoregions	Spalding <i>et al.</i> (2007)
Global biogeographic regions	Procheş (2005)
Sub-Saharan Africa	de Klerk <i>et al.</i> (2002)
Terrestrial ecoregions	Olson <i>et al.</i> (2001)

studies revise or recognize biogeographical regions based on models, but do not test if these global biogeographical regions are natural, that is, monophyletic. For example, Holt *et al.* (2013) recovered the Sclater–Wallace Neotropical region, which includes the entire South American continent. They also recognized the Nearctic and Palearctic, but shifted the traditional boundary between them (p. 75): ‘The regions of central and eastern Siberia are phylogenetically more similar to the arctic parts of the Nearctic region, as traditionally defined, than to other parts of the Palearctic [...] As a result, our newly defined Palearctic realm extends across the arctic and into the northern part of the Western Hemisphere’. This phylogenetic similarity allows the shifting of boundaries but does not test monophyly or naturalness of areas as it does not address the relationships among the areas. By relationship, we mean a shared history reflecting the shared history of the taxa that live in the areas, not a phenetic hierarchy of areas based on the similarity of the biotic composition of each area. What if some areas within the Nearctic are hypothesized to be more closely related to areas in South America than they are to any other Nearctic areas? If so, the Nearctic would not be a natural, that is, monophyletic biotic area. Monophyly is a key concept in comparative biogeography: it is the evidence for a natural classification. For example, if a named region has sub-areas that share closer relationships with sub-areas of another named region than to its own, neither region is natural. By natural we mean that the included biota share an historical relationship or biotic divergence (Parenti & Ebach, 2009). The phylogenetic signal within area relationships is an independent test of a natural area classification. The phylogenetic signal comes from the phylogenies of many different monophyletic taxa (or clades). Taxa that have cosmopolitan distributions or that are seemingly not affected by geographical barriers contribute little or no signal, in the same way that certain molecular and morphological characters may have little congruence with an overall phylogenetic signal. Area monophyly (geographical congruence) has been a fundamental principle of comparative biogeography since it began (Platnick & Nelson, 1978). Area monophyly is a positive test of proposed natural area classifications. In contrast, studies that propose areas and area classifications based on parametric models, theoretical constructs of species and areas and the expected or projected relationships between them (e.g. Biodiverse, a tool for the spatial analysis of biodiversity; Laffan *et al.*, 2010), do not include area relationships as inferred from the taxa that live in them.

Ironically, bioregionalization, although in its modern form digitized and computationally complex, has been criticized for not being complex enough, an echo from a previous century:

Compare:

... biogeographers must be aware that expert- and algorithm-drawn boundaries are ultimately only arbitrary, although helpful, constructs that are inherently limited in fully capturing the biogeographical complexity.

(Kreft & Jetz, 2013, p. 343)

with:

The facts of zoogeography are so involved, and often apparently contradictory, that a skilful dialectician with the requisite knowledge can make a plausible argument for antithetical postulates.

(Gill in Heilprin, 1883, pp. 270–271)

Biogeography tackles an intricate set of facts, some contradictory and seemingly intractable. Yet the challenge is no greater than that faced by phylogenetic systematics to which biogeography has turned for a method to separate natural from artificial areas.

## DISCOVERING NATURAL AREAS: AN ANALOGY FROM PHYLOGENETIC SYSTEMATICS

Biogeographical areas may be natural (monophyletic) or artificial (aphyletic; Ebach & Williams, 2010). Artificial areas – human constructs – may not be distinguished from natural biotic areas if the regions are defined but not tested (*sensu* Michaux, 2010). The method of treating the units of biogeography, areas, as units of classification (taxa), was developed during the cladistic revolution of the 1970s (Platnick & Nelson, 1978), but has influenced just a handful of studies in the modern bioregionalization revival (Ebach, 2013). Phenetic clustering and ordination are the dominant quantitative methods used to develop modern bioregionalizations (Kreft & Jetz, 2010; Table 1). Yet if clades are monophyletic, that is, natural, can we not say the same about biotic areas? By extending the analogy to biogeography, we recognize all taxonomically defined distributions – such as areas of endemism, subregions, regions and realms – as biotic areas. We can thus compare an area of endemism based on a single species with that based on several genera, and so on. When we extend all systematic terms to biogeography, we recognize analogous terms such as area and taxon, taxon monophyly and area monophyly (see Parenti & Ebach, 2009, box 2.2). Discovery in all historical science means finding patterns. Phylogenetic systematics is an historical science that relies on relationships among characters and taxa. For example, the character states a, b and c may form a relationship (a,(b,c)), which may be drawn as a character state tree. Combine two or more overlapping character state trees and you end up with an aggregate pattern, one that represents the shared relationships in each of the constituent character state trees. In systematics, we call the aggregate pattern a cladogram. Similarly, in comparative biogeography, area relationships form areagrams: cladograms in which the names of taxa are replaced by the areas in which they occur. Areagrams are analogous to character state trees in phylogenetic systematics. Areas that are not shared and do not contribute any information to area relationships may be discarded to form reduced areagrams. When we combine a series of overlapping areagrams or reduced areagrams, they may form an aggregate pattern or a general areagram, which represents the sum of area relationships or information within the areagrams (analogous to a cladogram in systematics, see Parenti & Ebach, 2009). These patterns may be summarized by hand, using a computer program such as LISBETH (Zar-

agüeta-Bagils *et al.*, 2013), or with conventional parsimony programs. Recent applications of this method to biogeography include Brown *et al.*, 2006 (Malesian archipelago), Escalante *et al.*, 2007 (Mexico and the Caribbean), Parenti & Ebach, 2009 (Indo-Pacific), Parenti & Ebach, 2010 (Wallacea), Hoagstrom *et al.*, 2014 (North American highlands) and Morrone, 2014b (the Neotropical region, see below).

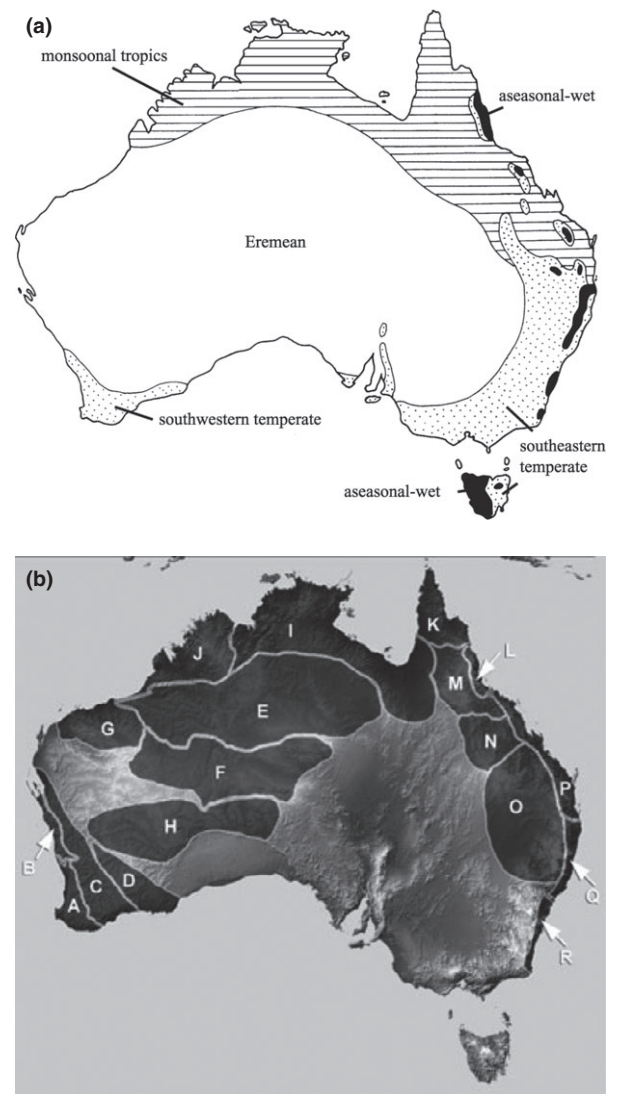
A general areagram, like a cladogram, represents discovery of natural taxon (area) relationship or (area) monophyly. This process of discovery may be hampered by how we describe areas in the same way that phylogenetic analyses suffer from poor taxon delimitation. Make the areas too large and they may incorporate unrelated areas, equivalent to aphyly in systematics (i.e. uninformative taxa due to paraphyly, polyphyly, monotypy, polytomy; see Ebach & Williams, 2010). Make the areas too small, and a different problem arises: there are few overlapping areagrams, hence no chance to discover a shared history. Although the former problem results from aphyly, the latter is solely about the limits of data. The molecular revolution in phylogenetic systematics has generated more and more cladograms at finer and finer spatial scales thereby making it possible to test whether more and more areas are monophyletic (see also Heads, 2014).

## DISCOVERING AND TESTING AREA RELATIONSHIPS AND CLASSIFICATIONS

### Australia

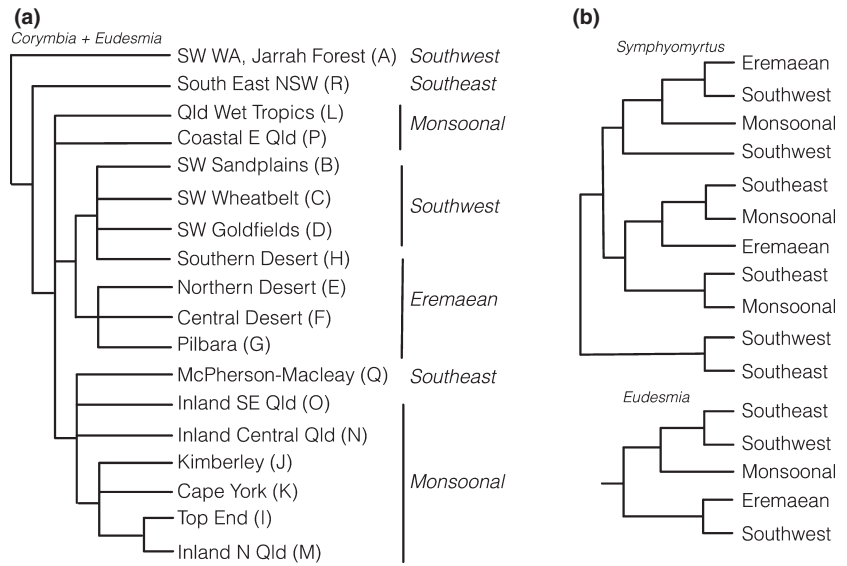
Australian bioregionalization has a rich history, including various attempts at terrestrial, freshwater and marine area classification over the last 150 years (Ebach, 2012). At first, many regions were recognized based on a mixture of similar geography, climate and organismal distributions. For example, the first set of areas for plants – the Eremaean, Euronotian and Southwest of Tate (1889) – are still used in modern biogeographical studies, albeit in different ways. The Eremaean may describe areas of endemism (based on taxonomic distributions) or biomes (based on the distribution of vegetation and climate). Few studies have asked whether these regions are natural (monophyletic).

We compare the analyses of Crisp *et al.* (2004) and Ladiges *et al.* (2011). Each starts with a phylogenetic hypothesis of *Eucalyptus* and then replaces a species name with the area in which it lives to discover area relationships. Each study adopts the same phylogenetic hypothesis of eucalypts, but has a different concept of areas: Crisp *et al.* (2004) adopts biomes based on Tate's (1889) original phytogeographical areas (Fig. 1a), whereas Ladiges *et al.* (2011) uses smaller areas of endemism based on the distribution of taxonomic groups (Fig. 1b), with five of their 18 areas falling with the Eremaean biome of Crisp *et al.* (2004). The areagrams of both are revealing (Fig. 2). In the areagram of Ladiges *et al.* (2011) (see Fig. 2a), each of the five 'Eremaean' regions falls into different clades, that is, they share closer relationships with other



**Figure 1** (a) The 'Map of Australian biomes (modified from Burbidge 1960; Schodde 1989)' from Crisp *et al.* (2004, fig. 1, p. 1552). (b) 'Areas of endemism defined on the basis of the eucalypt distributions' from Ladiges *et al.* (2011, fig. 2, p. 32). Figures used with permission.

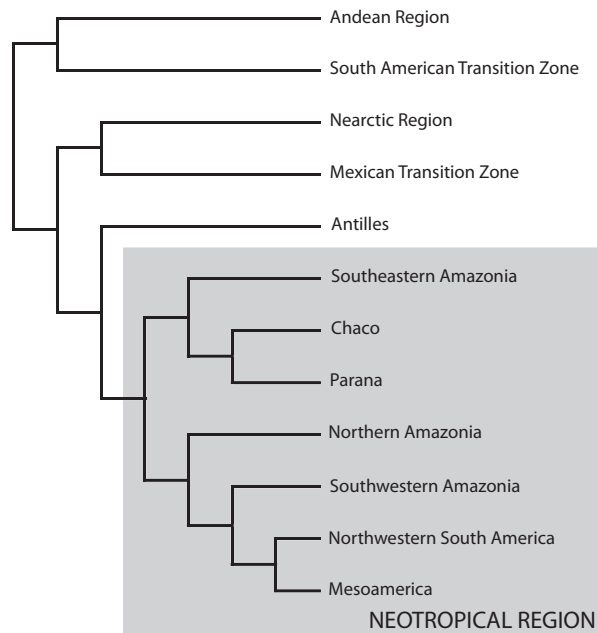
regions than they do with each other. Moreover, an additional eight areas fall into the monsoonal biome, four into the south-western biome and two into the south-eastern biome. This result is repeated in the areagrams of Crisp *et al.* (2004) (see Fig. 2b). That is, the Eremaean biome has an equally close relationship with both the south-western and south-eastern and monsoonal biomes, meaning that the Eremaean is aphyletic. The same is true for the monsoonal, south-western and south-eastern biomes. Both analyses demonstrate that none of the biomes of Crisp *et al.* (2004) falls into unique clades, meaning they are artificial and in need of revision. The biomes have failed the test for area monophyly. The biomes are uninformative in biogeographical studies in the same way that an aphyletic taxon, such as the Invertebrata, is uninformative in phylogenetic studies.



**Figure 2** (a) The general areagram of *Eucalyptus* (*Corymbia*) + *Eucalyptus* (*Eudesmia*) of Ladiges *et al.* (2011, fig. 2, pp. 32–34). (b) The reduced areagrams of *Eucalyptus* (*Symphyomyrtus*) and *Eucalyptus* (*Eudesmia*) of Crisp *et al.* (2004, table 1, fig. 1).



**Figure 3** The Neotropical region of Wallace (1876), divided into four subregions: Chilean, Brazilian, Mexican and Antillean.



**Figure 4** General areagram for a revised Neotropical region (shaded) and its outgroup areas (after Morrone, 2014b, fig. 5).

### The Neotropical region

The same philosophy and methods adopted from phylogenetic systematics were used to test the areas of the Neotropical region (Morrone, 2014b). The Neotropical region, as mapped by Wallace (1876) (see Fig. 3), comprised four subregions – Chilean, Brazilian, Mexican and Antillian – and spanned the entire South American continent as well as Mexico, Central America and the West Indies. Monophyly of the Neotropical region, in particular of the South American biota, has been contradicted repeatedly (see Morrone, 2002). The biota of southern South America from south of 30° S and the Andean region is more closely related to that of the Cape or Afrotemperate region of continental Africa and the temperate regions of Australia, New Guinea, New Caledonia and New Zealand than it is to the biota of tropical lowland South America (see also Moreira-Muñoz, 2007). Morrone (2014b) extracted information from cladograms of 36 taxa of invertebrates, vertebrates and plants distributed throughout 12 regions and summarized the aggregate relationships in a general areagram (Fig. 4). He redefined the Neotropical region *sensu stricto* to include just the tropical areas, not the Andean region and southern South America, as had many biogeographers over the past 150 years. The Neotropical region as traditionally conceived was rejected. Further, the Mexican Transition Zone and the portion of the Nearctic Zone in Mexico are more closely related to the Neotropical region *sensu stricto* than is the Andean and South American Transition Zone, *contra* the Neotropical and Nearctic regions of Sclater–Wallace, Holt *et al.* (2013) and many others. We note that Morrone’s (2014b) analysis is not a direct test of

monophyly of the Nearctic region as it included just one Nearctic area (the Nearctic Zone in Mexico).

Morrone (2014a) went one step further to present a detailed bioregionalization or classification of areas within the monophyletic Neotropical region. He followed the International Code of Area Nomenclature or ICAN (Ebach *et al.*, 2008), which outlines rules to name biogeographical areas analogous to those used to name biological taxa. Therefore, he included the name of the describer and date of the description in the formal name of each region e.g. Neotropical region Sclater, 1858, not Wallace who still gets all the credit. Despite the logic of this reclassification and its support from an array of taxa, there is reluctance among many biogeographers to alter the Sclater–Wallace classification to reflect global phylogenetic patterns.

### CONCLUSIONS

Simply naming an area does not ensure that it is natural, no matter what model one chooses. We discover a natural biogeographical area when we test it and corroborate its monophyly. A monophyletic area has great explanatory power as it represents a natural region formed by biological and geological evolutionary processes. Our job is to discover and test the world’s natural areas through aggregate patterns (i.e. general areagrams) and test area monophyly. As we relate for Australia and the Neotropical region, we have a method to propose and test area monophyly.

Many modern biogeographers do what Sclater, Wallace and their contemporaries could have only dreamt of: combine vast datasets and apply rational models to describe and classify the biogeographical regions of the world. A theory to assess objectively if these areas are natural did not exist in the late 19th century. The age of regionalization was placed on hold. Now, because we can test whether these areas are natural, the goals of 18th and 19th century plant and animal geographers can finally be realized – to discover the natural biotic areas of Earth and to understand their relationships.

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## BIOSKETCHES

**Malte C. Ebach** is a Senior Lecturer in the School of Biological, Earth and Environmental Sciences at UNSW Australia. Malte's research focuses on Australasian biogeography, the historical development of phyto- and zoogeography and natural classification.

**Lynne R. Parenti** is a Curator of Fishes and Research Scientist at the National Museum of Natural History, Smithsonian Institution, Washington, DC. She studies the systematics, biogeography and reproductive biology of bony fishes, collections-based comparative biology, and the theory and methods of biogeography.

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Editor: Richard Ladle