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Endemism in historical biogeography and conservation biology: concepts and implications

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SUMMARY

Endemism is often misinterpreted as referring to narrow distributions (range restriction). In fact, a taxon is said to be endemic to an area if it lives there and nowhere else. The expression "endemic area" is used to identify the geographical area to which a taxon is native, whereas "area of endemism" indicates an area characterized by the overlapping distributions of two or more taxa. Among the methods used to identify areas of endemism, the optimality criterion seems to be more efficient than Parsimony Analysis of Endemism (PAE), although PAE may be useful to disclose hierarchical relationships among areas of endemism. PAE remains the best explored method and may represent a useful benchmark for testing other approaches. Recently proposed approaches, such as the analysis of nested areas of endemism, networks and neighborjoining, are promising, but need to be more widely tested. All these methods attempt to identify biogeographically homogeneous sets of areas characterized by shared species, without any attempt to evaluate their relative importance for conservation purposes. Analyses based on weighted endemism methods identify areas of endemism according to specie distributional rarity and phylogenetic position, being thus appropriate for conservation purposes. The proportion of endemic species to the total number of species living a given area is the most frequently used measure to rank areas according to their relative endemism. However, proportions obscure differences in raw numbers that can be important in conservation biology. Because the number of (endemic) species tends to increase with area, some authors proposed to model the endemics-area relationship and to consider the areas displaced above the fitting curve (i.e. those having a positive residual) as hotspots. However, the use of residuals may lead to areas being identified as hotspots for almost every size class of richness. Thus, it is important to evaluate the ability of the hotspots recovered by these procedures to really conserve total (endemic) species diversity.

INTRODUCTION

Widely used concepts typically receive multiple (and generally contrasting) definitions. For example, the species concept, which is fundamental in biology, has been applied in a number of different ways and both biologists and philosophers disagree on the proper definition of the term "species" and its ontological status (e.g., Mayden 2007, Schulz et al. 2008).

Endemism is one of the most important concepts in biogeography and has a central role in conservation biology. However, the large variety of definitions and the lack of consistence in their applications make it a source of continuous misunderstanding and conflicting results.

In this paper, I present a review of: (1) the history of the concept of endemism; (2) the associate terminology; (3) some methods currently used to identify areas of endemism; and (4) the use of endemism in conservation biology.

THE CONCEPT OF ENDEMISM

The word endemic has been originally introduced in the French language (*endémique*) in a medical book by Suau (1586) and entitled *Traitez contenans la pure et vraye doctrine de la peste et de la coqueluche*. The word is a combination of the Greek words *ἐν* (in) and *δῆμος (*people) plus the suffix -*ique*. It was coined to indicate the constant and characteristic presence of a disease in a certain region.

The word "*endémique*" entered the English language as *endemical* and *endemick* in 1662 (with English translation by John Chandler of van Helmont's·*Oriatrike*: "It is not manifest, that Endemicks or things proper to People in the Countrey where they live, are drawn by the Arteries"). It seems that the form "*endemic*" was first used in 1759 (Goldsmith 1759: "A traveller in his way to Italy, happening to pass at the foot of the Alps, found himself at last in a country where the inhabitants had each a large excrescence depending from the chin, like the pouch of a monkey. This deformity, as it was endemic, and the people little used to strangers, it had been the custom, time immemorial, to look upon as the greatest ornament of the human visage").

The Italian adjective "*endemico*" seems to be first used in 1787 by Scuderi (*Memoria* […] *per servire alla intiera e perfetta estinzione del vajolo*). In fact, Vallisnieri already used the word "*endemio*" with the same meaning before 1730 (Vallisnieri 1733; the work was published posthumous – Vallisnieri died in 1730): "Termine Medico, tolto dal Greco *Endemios*. Significa un male famigliare a un popolo, quasi patrium dixeris, come la *Plica Polona* a Polacchi, lo Scorbuto a' Settentrionali, o ai popoli maritimi &c. È differente dall'*Epidemico*, il perché questo suole assalire solamente in certi tempi, o per l'aria infetta, o per i cibi, o acque di cattiva qualità, o simili cose a tutti comuni". However, "*endemio*" was superseded by "*endemico*".

It seems that the word "*endemico*" has been long used very rarely. For example, it is recorded by the *Vocabolario degli Accademici della Crusca* (the first Italian dictionary), only in 1863 (fifth edition).

The word "*endémique*" served as a root for a variety of other, correlated words, among which "*endemism*". According to the *Trésor de la langue Française informatisé* (http://atilf.atilf.fr/tlf.htm) the French "*endémisme*" is dated to 1908, when it appeared in a famous book of geography by Paul Vidal de La Blache. However, since the Italian "*endemismo*" is recorded at least from 1892 (De Mauro 1999), it is very probable that "*endémisme*" was used in French long before 1908. We could not ascertain when "*endemism*" was introduced into the English language.

The French "*endémicité*" first appeared in 1844 (De La Berget et al. 1844**)**, and the Italian equivalent "*endemicità*" before 1859 (Boccardo 1859).

The French word "*éndémie*" (first recorded in 1495, in Le Forestier's *Le régime contre epidimie et pestilence*) and its Italian equivalent "*endemia*" (first recorded in 1855, in Fanfani's *Vocabolario della lingua italiana*) have been used very rarely and are now completely disappeared.

The word "endemic" was transferred form the medical to the biological language by De Candolle (1820: 54), who used the expression "*genres endémiques*" (endemic genera) to indicate plant genera whose species are all grouped in one region.

It is interesting to note that the Italian word "*endemismo*", as clearly indicated by the suffix –*ismo*, refers to a phenomenon, yet it is frequently (but incorrectly) used to indicate an endemic taxon (i.e. in the sense of the English "*endemic*" used as a noun). The Italian word corresponding to endemic and which should be used to indicate an endemic taxon is "*endemita*" (plural: "*endemiti*"), although this word is rarely used.

Endemism refers to the exclusive occurrence of a species in a defined geographical area. Therefore, the concept of endemism depends on the spatial scale considered. Thus, it is perfectly correct to say that the tenebrionid *Probaticus cossyrensis* Sparacio, 2007 is endemic to the Island of Pantelleria, that the proteus *Proteus anguineus* Laurenti, 1768 is endemic to the Dinaric Alps, and that the African elephant *Loxodonta africana* Blumenbach, 1797) is endemic to Africa (and that, ultimately, all species are endemic to the Earth). Although the term has been used also to define species restricted to small areas, endemism is not linked to the size of area.

The endemism concept is merely phenomenological and different taxa can be endemic to the same area as a result of completely different historical processes. To express a temporal dimension, Engler (1882) introduced the words "*palaeoendemic*" and "*neoendemic*". The use of these words, however, varies among authors. For example, some authors use "*palaeoendemics*" for ancient taxa that were formerly wider distributed and became isolated because of range contraction and/or the extinction of close relatives, and "*neoendemics*" for taxa that have evolved relatively recently and have not yet had an opportunity to spread beyond their current limits (e.g., Cox and Moore 2010, Biondi 2016). By contrast, other authors use "*palaeondemics*" and "*neoendemics*" to indicate taxa that evolved in the distant past and in fairly recent times, respectively, with no implications about their former ranges (Lomolino et al. 2010).

Recently, Myers and De Grave (2000) proposed a complex nomenclature to distinguish among different types of endemics, which can be summarized as follows:

Holendemics: Taxa limited only by ecological and physiological tolerance. Holendemic taxa typically have good dispersal and colonization powers, which allow them to assume wide distributions, provided that a sufficient time for spreading and establishment is given.

Euryendemics: Taxa with broad, more or less continuous or contiguous distributions, limited by biogeographical barriers. Euryendemic taxa typically show dynamic ranges (i.e. they are expanding or contracting their ranges, or are in a quasi stasis)

Stenoendemics: Taxa with restricted, more or less continuous or contiguous distributions, limited by biogeographical barriers. Stenoendemic taxa include taxa that evolved *in situ* from a clade constrained historically by biogeographical barriers, are relict taxa, or evolved recently, with no sufficient time to expand their range.

Rhoendemics: Taxa with two or more widely disjunct distributions. Their disjunct distributions can be due to either vicariance or jump dispersal. Taxa that have disjunct distributions as a result of vicariance events can be divided into two types: *euendemics* and *cryptoendemics*. Euendemics are taxa isolated by tectonic changes in geography, whereas cryptoendemics are isolated by extinction of intervening populations or taxa. The lack of cladistic reconstructions for most taxa makes it generally impossible to distinguish between euendemics and cryptoendemics, but when the information is available this distinction might be useful for interpreting the history of areas.

Another interesting classification of various types of endemics has been proposed by Favahger and Contandriopoulos (1961) for plants on the basis of their evolutionary history:

Palaeondemics: taxa systematically isolated.

Patroendemics: taxa that have not varied in a given region, but that, in other regions, have given rise (by polyploidization) to more recent taxa, the area of which is generally much larger.

Schizoendemics: taxa that result from the slow and progressive differentiation of a primitive taxon into different parts of its range.

Apoendemics: taxa that originated in a given region (by polyploidization) from a diploid taxon, which is widespread in neighbouring countries.

Cryptoendemics: taxa that can be distinguished from their relatives inhabiting adjacent regions only on the basis of their different chromosome numbers.

Note the particular meaning that the words "palaeondemic" and "cryptoendemic" in a very different sense compared with Favahger and Contandriopoulos' (1961) use.

Finally, "*microendemic*" and "*stenoendemic*" are commonly used words to indicate taxa with a very restricted distribution.

METHODS TO IDENTIFY AREAS OF ENDEMISM

Endemism in historical biogeography

Historical biogeography attempts to explain geographical distributions of taxa in terms of their history rather than exclusively in terms of their current ecology. In fact, the scope of historical biogeography is twofold: (1) to explain current patterns of the distribution of monophyletic groups in terms of their phylogeny (taxon history), and (2) to reconstruct earth history on the basis of shared historical information recovered from phylogenies of different taxa (earth history). Several methods have been proposed for taxon history analysis, which rely on the same basic approach: an area cladogram is constructed by substituting taxon labels for their host areas (area coding) and historical relationships between area relationships and taxon relationships are deduced. By contrast, the various methods used in earth history analysis are based on the following basic approach: different area cladograms are compared by seeking a common history through the analysis of the phylogenies of the taxa that live there.

In the "earth history" program of historical biogeography, the fundamental units of analysis are called "areas of endemism", i.e. areas characterized by the overlapping distributions of two or more taxa (at least two, because an area occupied by just one taxon will have no history shared with any other area). The expression "area of endemism" is frequently used as synonymous with "endemic area". The semantic distinction between these two expressions (see Tables 1 and 2) is made clear in the hearth history approach proposed by Parenti and Ebach (2009) with the label of "comparative biogeography". Comparative biogeography, as defined by Parenti and Ebach (2009), aims at identifying biologically meaningful areas, called "endemic areas" and at organizing them in a classification scheme according to their relationships. These relationships are inferred from the phylogenies and distributions of the taxa that inhabit the focal areas. The biogeographical classification is a hierarchy incorporating increasingly encompassing areas, such as districts, regions, and realms, which form biotic areas.

The approach of Parenti and Ebach (thereafter referred to as P&E approach) is similar to that of modern systematics. In systematics, taxa are organized into monophyletic groups based on homologs (i.e. structures that are found in inclusive groups of organisms, even if in different forms). In P&E approach, areas are organized into monophyletic groups (i.e. areas that share the same biological and geological history) and, for this, phylogenies of their taxa are analysed to find area homologies. As a single character cannot be informative of phylogenetic relationships, so a single phylogeny is not useful to reconstruct area relationships, but can be deduced only by comparing multiple phylogenies. The basic unit in biogeography, which can be considered an equivalent of the species concept in systematics, is the "endemic area". A group of endemic areas forms a "biotic area" (as a group of related species forms a higher taxon). The definition of endemic areas and their recognition are as difficult as the definition and recognition of species.

In P&E's terminology, an endemic area is any disjunct or continuous geographical space, through time, that delimits the current and past distribution of one or more taxa. Thus, the concept of an endemic area may be restated simply as the place (geographical area) to which a clade or a biota is understood to be native.

By contrast, in P&E's terminology, an area of endemism is an area characterized by the overlapping, or congruent, distributions of two or more taxa. As an example, let us consider a genus of fish including three allopatric species, one each that lives in Africa, South America and Australia. A genus of beetle may include two allopatric species, living in Africa and South America, respectively. Africa and South America are areas of endemism for the two genera and we can investigate their biogeographical relationships. Australia is an endemic area for the species of fish that lives there, but it is not an area of endemism in this hypothetical study because its relationship cannot be part of a pattern that may be shared between the fish and the beetle.

Table 1. Definitions of endemic area (modified from Parenti and Ebach 2009)

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Definition	Author(s)
Region to which an organism is particular	Clements 1905
Distributions of individual species	Polunin 1960
Area delimited by coincident distributions of taxa that occur nowhere else	Nelson and Platnick 1981
Delimited or restricted distribution of a single taxon	Hinz 1989, *sensu* Dansereau 1957 (see Anderson 1994)
Congruent distributional limits of two or more species	Platnick 1991
Region occupied by a monophyletic group of organisms or a species found only there	Humphries and Parenti 1986
"Area of occurrence": biogeographical region occupied by a monophyletic group of organisms or a species.	Harold and Mooi 1994
A taxon (e.g., a species) is considered endemic to a particular area if it occurs only in that area	Crisp et al. 2001
Area delimited by geographical barriers, the appearance of which entails the formation of species restricted by these barriers	Hausdorf 2002
Geographical distribution of a taxon within its physical range and ecological boundary	Ebach and Humphries 2002
An area recognized by the coincident restriction of two or more taxa	Laffan and Crisp 2003
An area in which numerous species are endemic	Szumik and Goloboff 2004
An area containing species not living elsewhere	Domínguez et al. 2006
The smallest area with significantly congruent distributions recognized as significantly different from all other areas at a particular level in nested clade analysis (NCA)	Deo and DeSalle 2006

Table 2. Definitions of area of endemism (modified from Parenti and Ebach 2009).

Definition	Author(s)
Regions where populations evolved in isolation	Rosen 1978
Areas that demonstrate distributional congruence of constituent taxa	Cracraft 1985
Area occupied by two taxa, with overlapping area identifi ed as a separate area	Axelius 1991
Smallest coincident ranges of two species and the geographical extent of forest islands	Griswold 1991
Area defined by the congruent distributional limits of two or more species. 'Congruent' in this context does not demand complete agreement on those limits, but relatively extensive sympatry	Platnick 1991; see also Morrone and Crisci 1995, Linder 2001a
A geographical region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such defined regions. This definition demands, minimally, a three-taxon statement for each group, with each taxon of each group occurring in an area of endemism.	Harold and Mooi 1994
Smaller generalized tracks	Morrone 1994a
Areas of non-random distributional congruence among different taxa	Morrone 1994a
Extensive co-occurrence of biotic elements (*sensu* Hausdorf 2002)	Mast and Nyffeler 2003
Areas where the distributions of at least two taxa overlap	Quijano-Abril et al. 2006

Areas of endemism are hierarchically arranged, with smaller areas of endemism nested within larger ones (Morrone 2009, Crother and Murray 2013, 2014), and their relationships can be therefore organized in a systematic structure. However, some degree of overlap among areas of endemism can occur, particularly in transition zones (Morrone 2014).

A taxon that lives in more than one area of endemism is called widespread, whereas a taxon that lives only in one area of endemism is called endemic to that area. The species originating in an area of endemism by vicariance form a biotic element, i.e. a group of taxa whose ranges are more similar to each other than to those of other such groups (Hausdorf 2002).

Endemic areas are the building blocks of comparative biogeography and the identification of areas of endemism is fundamental for biogeographical regionalization (Rosen and Smith, 1988; Parenti and Ebach 2009), i.e. the hierarchical arrangement of areas of endemism within a system of realms, regions, dominions, provinces and districts (Ebach et al. 2008, Parenti and Ebach 2009).

P&E approach is addressed to reconstruct relationships among areas of endemism, and therefore belongs to the field of historical biogeography. With the more descriptive aim of identifying areas of endemism and their relationships (without historical implications), there are several alternatives available, e.g., phenetic clustering (e.g., Linder 2001a, Moline and Linder 2006), parsimony analysis of endemicity and cladistic analysis of distributions and endemism (e.g., Morrone 2013), nested areas of endemism analysis (Deo and DeSalle 2006), endemicity analysis (Szumik et al. 2002, Szumik and Goloboff 2004), analysis of biotic elements (Hausdorf and Hennig 2003), sympatry networks (Dos Santos et al. 2008) and network analysis (Torres-Miranda et al. 2013). These approaches are discussed in the following sections.

Parsimony Analysis of Endemicity

The first, and most commonly used approach to identify areas of endemism, is the Parsimony analysis of endemicity (PAE). This method was originally introduced by Rosen (cf. Rosen 1984, 1988a, b, 1992, Rosen and Smith 1988) for examining presence/absence data of taxa by areas to define regions with shared presence of taxa. PAE may be considered to be similar to phenetic clustering, although the former creates groups based only on shared presences using a cladistic approach, whereas the latter uses overall similarity (Rosen and Smith 1988, Waggoner 1999, Fattorini and Fowles 2005, Wiley and Lieberman 2011).

In the PAE, the areas are treated as traditional taxa (areas-as-taxa) and the distributions of the taxa serve as the characters (taxa-as-characters). The PAE groups areas by their shared taxa according to the most parsimonious cladogram(s). If more than one most parsimonious cladogram is found, a consensus cladogram is calculated. Therefore, PAE attempts to minimize both ‘‘dispersion events’’ (parallelisms; i.e. occurrence of the same taxon in areas of different origin) and ‘‘extinctions’’ (secondary reversions, i.e. absence of taxa in related areas).

In PAE, any taxon occurring in more than one area helps to illuminate the relationship between the areas, hence, is an informative taxon-as-character. Thus, shared taxa act as ‘synapomorphies,’ or ‘synendemics’ (Rosen 1992). By contrast, taxa found in a single area are equivalent to autapomorphies, being uninformative for assessing relationships. Characters are typically coded as 0 (absence) or 1 (presence); some authors have used ‘?’ for doubtful presences (Smith 1992, Echeverry and Morrone 2010).

Characters are usually polarized using a hypothetical area with all zeroes as the outgroup (e.g., Vargas et al. 1998, Glasby and Alvarez, 1999, Vega et al. 1999, Bisconti et al. 2001). As a result of this polarization, areas having few taxa will tend to be viewed as being primitive. However, as observed by Glasby and Alvarez (1999), absence may be the result of (1) taxon never occurred in sample area, (2) taxon became extinct, or (3) taxon not yet been discovered. To reduce these problems, Fattorini (2002) suggested using Dollo parsimony. Because according to the Dollo parsimony 1->0 is more likely than 0->1, also absences because of incomplete knowledge are easily considered as homoplastic characters. Dollo optimization was also used by Rosen and Smith (1988), Glasby and Álvarez (1999), Unmack (2001) and Fattorini and Fowles (2005). Enghoff (2000) suggested performing the analysis with irreversible characters

to avoid having branched supported by reversals (interpreted as extinctions), which is meaningless. Cano and Gurrea (2003) and Ribichich (2005) used an outgroup area coded as all ones, which means that areas underwent a biotic impoverishment through time starting from a cosmopolitan biota (Rosen and Smith, 1988, Cecca, 2002). Vázquez-Miranda et al. (2007) used a real area as an outgroup, whereas Rosen and Smith (1988) and Crother and Murray (2013) suggested that it was possible to work with an unrooted cladogram. PAE is usually performed using equal weights, thus all species occurrences are coded as 1. To emphasize the importance of species with restricted range, and hence to reduce homoplasy caused by widespread species, Linder (2001b) suggested weighting species inversely to their distribution. Similarly, analyses with implied weights (Goloboff, 1993) have been undertaken (Luna-Vega et al. 2000, Escalante et al. 2007a, Aguirre et al. 2011, Ribeiro and Eterovic, 2011).

The units used in PAE are predetermined areas of any kind, such as arbitrary operational units (van Soest, 1994), quadrats (Morrone 1994a, Linder 2001a,b, García-Barros *et al.* 2002, Morrone and Escalante 2002, Rovito *et al.* 2004, García-Barros, 2003, Rojas-Soto et al. 2003, Vergara et al. 2006, Herrera-Paniagua et al. 2008, Meng et al. 2008, Löwenberg-Neto and de Carvalho, 2009, Ramírez-Barahona et al. 2009), islands (Bisconti *et al.* 2001, Trejo-Torres and Ackerman 2001, Fattorini 2002), localities (Raxworthy and Nussbaum, 1996, Ron 2000, Anstey et al. 2003, Ribichich, 2005, Navarro et al. 2007, Ramírez-Arriaga and Martínez-Hernández, 2007, Gates et al. 2010, Aguirre et al. 2011), interfluvial regions (Silva and Oren 1996), hydrological basins (Aguilar-Aguilar *et al.* 2003, Huidobro et al. 2006), politically defined areas (Cué-Bär et al. 2006, Nelson 2008, Ribeiro and Eterovic 2011), biogeographical areas (Glasby and Alvarez 1999, Vega et al. 1999), predefined areas of endemism (Goldani et al. 2002, Katinas et al. 2004, Espinosa et al. 2006, Albert and Carvalho 2011). In a few analyses, latitudinal (Morrone et al. 1997, García-Trejo and Navarro 2004, Mihoč et al. 2006, Moreno et al. 2006, Espinosa-Pérez et al. 2009) or elevational (Trejo-Torres and Ackerman 2002) transects have been used.

Although the use of artificially delimited areas in PAE has been particularly criticized (Niehi 2006), quadrats can be appropriate when the aim of the study is to recover areas of endemism, because their use does not rely on predetermined, putatively historical areas as the units of analysis, whose identification is usually the goal of the analysis. Morrone (1994a, 2014) recommended the use of predefined quadrats when PAE is applied to delineate areas of endemism based on the presence or absence of taxa (see also Posadas 1996, Linder 2001a).

Results of PAE can be inconsistent if the matrix includes unrelated areas and/or taxa that have different histories. For this reason, some authors proposed to partition the data matrix into separate sets (e.g., Cracraft 1991, Myers 1991, Morrone 1998, Ron 2000, García-Trejo and Navarro 2004, Fattorini 2009, Watanabe 2012). When applied to paleontological data, data from different geological intervals or stratigraphical horizons are analysed separately (Rosen and Smith 1988, Smith and Xu 1988, Rosen and Turnsek 1989, Fortey and Cocks 1992, Geraads 1998, Aguirre et al. 2011).

As any other biogeographical analysis, PAE results are influenced by the degree of knowledge of species distributions. Gaps in species distribution data lead to false absences that biase area relationships. To overcome the shortcomings of poorly sampled areas, some authors used potential distributions based on niche modelling (e.g., Espadas Manrique et al. 2003, Rojas-Soto et al. 2003, Rovito et al. 2004, Escalante et al. 2007a, b, Gutierrez-Velazquez et al. 2013). Other authors have used a panbiogeographical approach building individual tracks before compiling the data matrix and then coding species as present when an individual track was present throughout all the sample areas or crossed a given biogeographical unit (e.g., Espinosa-Perez et al. 2009, Echeverry and Morrone, 2010, 2013). The simplest solution to cope with fragmented knowledge is using coarse maps (i.e. larger units), but this may lead to a loss of information.

Although PAE works under the 'total evidence' approach, some authors have suggested methods to reduce noises. Roig-Juñent et al. (2002) pruned grid cells that were found to be conflicting in a preliminary analysis. Gutiérrez-Velázquez et al. (2013) applied a co-occurrence analysis to filter those species that showed no significant co-occurrence.

PAE is usually applied using species, but there are examples of applications with genera or other supraspecific categories (Rosen 1988a, b, Rosen and Smith 1988, Rosen and Turnšek 1989, Fortey and Cocks 1992, Davis et al. 2002, Silva and Gallo 2007, McCoy and Anstey 2010).

The PAE cladogram can either be interpreted as a pattern of ecological similarities among areas or as reflecting historical patterns that were due to geological change (Rosen 1988a, 1992). According to Cracraft (1994), speciation by vicariance and biotoic dispersion produces historically structured (hierarchical) species assemblages, while long-distance dispersal results in non-hierarchical species assemblages. Thus, to test whether PAE results are due to ecological similarity or common history, i.e. if they are hierarchical or not, they can be compared with geological information (e.g., Waggoner 1999). Congruence between area cladograms and palaeogeographical reconstructions is evidence for vicariance and biotic dispersion, whereas incongruence is likely to reflect dispersal and/or ecological factors (cf. Rosen 1988a, Glasby and Alvarez 1999).

However, interpretations of the results vary, and the analysis may be considered to recover areas of endemism, biotic affinities, or area relationships (Morrone 2014). Although patterns identified by PAEs are usually interpreted in a static way, availability of PAE cladograms obtained at different time periods may also allow dynamic interpretations (Cecca 2002, Nihei 2006, Cecca et al. 2011).

PAE arranges areas hierarchically, but it is questionable if nestedness is really a general property of areas of endemism. Hovenkamp (2014) argued that the hierarchical nature of such areas is a methodological artefact of PAE.

Another disputed issue is if PAE cladograms should be defined by at least two taxa. According to Crother and Murray (2011, 2013, 2014) areas of endemism can be legitimately identified even when they do not contain unique species, provided that they host a unique combination of species.

To identify all possible subareas characterized by congruent occurrence of endemic species, Luna-Vega et al. (2000) and García-Barros et al. (2002) proposed, independently, a procedure known as parsimony analysis of endemicity with progressive character elimination (PAE-PCE). With this procedure, once the parsimony analysis has identified the most parsimonious cladogram(s), those species that are found to define groups of areas in the first analysis (i.e. species analogous to non-homoplasious characters acting as synapomorphies of sets of areas) are deleted, and a new search is started by repeating the analysis. A new set of cladograms is thus obtained that includes areas of endemism that were incongruent with those obtained in the former analysis. This procedure is repeated until no more endemism areas supported by at least one apomorphic species is found, i.e. until no more species support any clade. This approach has been used, among others, by García-Barros (2003), Huidobro et al. (2006), Vergara et al. (2006), Corona et al. (2007), Zamora-Manzur et al. (2011) and, in a panbiogeographical framework, by Echeverry and Morrone (2010, 2013) to find nodes or composite areas as areas where different generalized tracks (corresponding to the alternative clades obtained in different analyses) overlap.

Character evolution (i.e. changes in taxon distribution) on the area cladograms is rarely examined in PAE studies. Smith (1992), Geraads (1998) and Escalante et al. (2007a) used the ACCTRAN (accelerated character transformation) option, which gives a preference for a single origin followed by reversal, so that secondary losses of a taxon are made more likely than independent evolution. An opposite choice would be the use of the DELTRAN (delayed character transformation) option. DELTRAN gives a preference for two origins of a character state (parallelism). When taxa are used as characters, DELTRAN leads to a preference for dispersal, whereas ACCTRAN for vicariance.

To statistically testing the relationships of areas obtained from a PAE and their boundaries, Deo and DeSalle (2006) introduced the "nested areas of endemism analysis" (NAEA), which is a biogeographical adaptation of the nested clade analysis approach utilized primarily in genetic analysis of phylogeographical patterns (Templeton 1998).

Cladistic Analysis of Distributions and Endemism

Many authors have proposed more or less profound modifications of PAE and that they believed deserved new names, such as parsimony analysis of shared presences (Rosen and Smith, 1988),

parsimony analysis of distributions (Trejo-Torres and Ackerman 2001), parsimony analysis of species assemblages (Trejo-Torres and Ackerman 2002), parsimony analysis of community assemblages (Ribichich 2005), and cladistic analysis of distributions and endemism (Porzecanski and Cracraft 2005). I discuss here the cladistic analysis of distributions and endemism (CADE).

CADE was originally described by Cracraft (1991) as an alternative to PAE by including taxonomic hierarchy. Craw (1989), Cracraft (1991) and Myers (1991) independently suggested combining species and supraspecific taxa in order to incorporate phylogenetic information in a parsimony analysis of endemicity. This approach has been followed by several authors (Morrone 1994b, 1998, De Grave 2001, Luna-Vega et al. 2001, Morrone and Márquez 2001, Escalante et al. 2003, McInnes and Pugh 2007, Santos et al. 2007, Sánchez-González et al. 2008, Zamora-Manzur et al. 2011). Porzecanski and Cracraft (2005) provided a detailed description of this method, clarified its distinction from PAE, called it "cladistic analysis of distributions and endemism" and provided an application to South American areas of endemism. An application to the central eastern African mountains using flightless insects was given by Fattorini (2007a).

The basic difference between the PAE of Rosen and CADE is that the latter incorporates cladistic information by coding distributions for more inclusive hierarchical levels, e.g., species and their genera. Thus, even if present-day taxonomic knowledge does not resolve the detailed relationships among the species in a given genus, their more recent common ancestry relative to species in other genera implies a pattern of area relationships that can be incorporated into the analysis by coding the hierarchical level above them, in this case the genus.

According to the proponents of CADE, areas of endemism must be predetermined, based on congruence of distributions across the target taxa, with the purpose to extract historical relationships among these areas, not among sample localities. The notion of areas of endemism, unlike that of collecting localities, implies a putative common history for the members of these biotic assemblages, and recognizes the influence of history on common distributional pattern. As a result, CADE would be expected to minimize the clustering of areas based solely on ecological similarity, a possible weakness of PAE studies (Rosen 1988a).

In developing his CADE, Cracraft (1991) observed that if elements of biotas were subject to a common history of vicariance over time, raw distribution patterns should contain hierarchical information about that history. This is based on a general assumption of vicariance biogeography, namely that dispersion first leads to relative degrees of cosmopolitanism in biotas, that some of the taxa then differentiate in response to vicariance events, and finally these events divide the biota into areas of endemism. Thus, a taxon shared between two areas of endemism might be taken as evidence of their close relationship relative to a third area in which the taxon is absent. If long-distance dispersal has a minor role in structuring the areas of endemism of biotas, then raw distributions should be expected to carry historical information, because they were more profoundly shaped by past land configurations than recent ecological conditions (Fattorini 2006). By contrast, if the taxa under study have a high dispersal power, long distance dispersal may erase the historical signal present in raw distributional information. For example, Porzecanski and Cracraft (2005) showed that most important sources of noise in CADE might come from species that have recently expanded their ranges into neighbouring areas, and that such ecological noise can be removed if taxa subject to long-distance dispersal are excluded. Thus, CADE would work better with taxa characterized by low vagility (Fattorini 2007a).

Several authors have criticized PAE (Humphries 1989, Humphries and Parenti 1999, Enghoff 2000, Szumik et al. 2002, Brooks and van Veller 2003, Santos 2005, Nihei 2006, Garzón-Orduña et al. 2008, Peterson 2008, Carine et al. 2009, Casagranda et al. 2012), while others have defended it (Morrone 2009, Echeverry and Morrone 2010, Crother and Murray 2013, 2014, Morrone 2014). Because of their similarity, PAE and CADE have been usually confused and criticisms did not distinguish between the two methods. For example, Brooks and van Veller (2003) and Santos (2005), criticized PAE, pointing out that: (1) PAE will only recover correct historical relationships when species undergo a particular combination of vicariance and non-response to vicariance; (2) it does not use any phylogenetic information; (3) areas may be grouped together by shared absences but character change is

not examined; and (4) it is susceptible to being misled by shared episodes of postspeciation dispersal. Porzecanski and Cracraft (2005) noted that criticisms (1) and (4) are in fact problems shared by all methods of historical biogeographical analysis, including Brooks' parsimony analysis (Brooks et al. 2001) and component analysis (Morrone 2009). Problems due to the lack of phylogenetic information (criticism 2) apply much more to PAE than to CADE. Criticism 3, above, identifies a problem that can affect any parsimony method, but it is not correct to assume that groups based on shared absences will necessarily go undetected. Examination of character optimizations is always advisable in any parsimony method and the informative and 'homoplastic' taxa for any given area relationship can be identified. Fattorini (2007a) suggested to reconstruct character (taxon distribution) states at internal (ancestral) nodes on the area cladogram of a CADE using the ACCTRAN (accelerated character transformation) option.

Humphries (1989), Humphries and Parenti (1999), Parenti and Ebach (2009) and Santos (2005) consider PAE to be not a cladistic biogeographical method, because it does not take into account the phylogenetic information (a problem that is, at least in part, surpassed by CADE), and Brooks and van Veller (2003) concluded that PAE is the least defensible and least desirable of all cladistic biogeographical methods. However, these critiques do not disprove its use to identify areas of endemism. Garzón-Orduña et al. (2008) also concluded that PAE is not adequate to recover historical patterns, but it may be a useful tool for identifying areas of endemism. An analysis of the relationships between PAE and other related methods used in historical biogeography is provided by Morrone (2014).

Endemicity Analysis With Optimality Criterion

According to Szumik et al. (2002), a method used to identify areas of endemism must consider the taxa occurring in a given area and their positions in space. To take into account this spatial component, Szumik et al. (2002) proposed an explicit criterion of optimality that identifies areas of endemism by assessing the congruence among species distributions, which they termed "endemicity analysis" (EA). This approach has been further developed and implemented in the NDM-VNDM software (Goloboff 2004, Szumik and Goloboff 2004), which searches for areas of endemism as sets of cells that maximize endemicity scores by modifying (with trial-and-error) the original observed distributions of the species.

With this approach, the study region is divided into cells, and the congruence between a species distribution and a given area is measured by an endemicity score (*V*); then, the endemicity value of an area (*E*) is calculated as the sum of the V values of the species included in the area.

The endemicity score of individual species takes into account the following elements:

- number of cells of *A* in which species *j* is actually present (*p*);
- cells in which species is not present but "inferred as present" (*i*);
- cells of *A* in which species is assumed to be present (*a*);
- size of *A* (= number of cells conforming it) (*S*);
- cells outside *A* (but adjacent to it) in which species has been observed (*o*);
- same, in which species has been assumed (*d*);
- cells outside *A* (non-adjacent) in which species has been assumed (*n*).

Parameters *i*, *a*, *o*, *d*, *n* are weighted by factors *F*, which are used to make the corresponding terms more or less influential. In other words, the *F* factors determine if an apparently empty cell is in fact occupied according to their distance from occupied cells.

The resulting formula to calculate the endemicity value of an individual species *j* is:

$$Vj = \frac{p + (iF_i) + (aF_a)}{S + \frac{o}{F_o} + \frac{d}{F_d} + \frac{n}{F_n}} \qquad \text{(eq. 1)}$$

Thus, with this approach, a species absent from one cell, but present in surrounding cells, can be considered as present. "Inferred" presences are different from "assumed" presences. "Assumed" records are given prior to the analysis (and thus become part of the "data"), whereas the "inferred" records are postulated by the method itself, as part of the analysis.

A possible concern in the above formula is the dependence of the size and shape of the set of cells that are used in calculations. Szumik and Goloboff (2004) report the following example: consider two sets of the same size, 9 cells, but different shape: a zig-zag line and a square of 3×3 cells. In the first case, there are 33 cells outside the area but adjacent to it; in the second, there are only 16. Finding 4 extraneous adjacent records outside the first area (i.e. 4 out of 33) is less disturbing than finding 3 records outside the second. To take into account this problem, they proposed considering the ratio between the sum of *o* and *d* (divided by their factors) and the edge size, *G*:

$$V_j' = \frac{p + (iF_i) + (aF_a)}{S + \frac{n}{F_n}} \times \left(1 - \frac{\frac{o}{F_o} + \frac{d}{F_d}}{G}\right) \quad \text{(eq. 2)}$$

The detection of areas of endemism is based on searching for areas (combinations of cells) with high scores of endemicity, calculated as:

$$E = \Sigma V_j \quad \text{(eq. 3)}$$

Two factors contribute to the *E* value: the number of species included in the area and the degree of congruence (measured by the *V* scores) between the species distributions and the area itself.

The program NDM-VNDM (Goloboff 2004, Szumik and Goloboff 2004) is designed to handle large datasets and searches for cell combinations that maximize *E*, by using either exact (implicit enumeration) algorithms, or heuristic (hill-climbing) searches.

Because minor variations (i.e. addition or deletion of a cell) produce minor or no differences in the E scores, the method can produce a large number of similar sets of cells. Thus, it is necessary to summarize these results in some way (Aagesen et al. 2013). For this, "consensus" areas can be calculated by putting together those areas that share a certain percentage of endemic species. For example, Bertelli et al. (2017) formed consensuses by adding a new area to the set of areas to overlap, if it shares 50% (or more) of its endemic species with any one of the areas already present in the set. This approach merges fewer areas into each consensus than adding an area when it shares the defining percentages with every one of the areas already present in the set (see Aagesen et al. 2013).

Szumik et al. (2002) criticized the use of PAE for identifying areas of endemism because it lacks an explicit optimality criterion. However, comparative studies show that areas of endemism recovered by PAE are consistent with those identified by using the optimality criterion, despite the methods are based on completely different procedures. This suggests that PAE and the analysis of endemism based on the optimality criterion might be reciprocally illuminating.

Casagranda et al. (2012) found that the analysis conducted with the optimality criterion performed better than PAE in noisy conditions. Carine et al. (2009) carried out an analysis comparing phenetic clustering (UPGMA), PAE and the optimality criterion, finding that the optimality criterion performed better than UPGMA and PAE and proposed it as the most appropriate method to identify areas of endemism.

A comparative study on the areas of endemism for Mexican mammals (Escalante et al. 2009) also showed that the endemicity analysis performed with the optimality criterion provided a better resolution than PAE, allowing the identification of several areas of endemism that were not detected by PAE. Moreover, performance of PAE decreases as the incongruence among the species distributions increases (Casagranda *et al.* 2012). However, PAE offers the advantage of organizing areas of endemism into a hierarchical scheme. An important merit of the optimality criterion is that it allows the identification of partially overlapping areas when they have different sets of endemic species. This is not allowed by PAE.

According to Escalante (2015) comparisons between PAE and the endemicity analysis with the optimality criterion are based on criteria (such as the number of areas found by each method, the number of endemic taxa, and the degree of congruence with predefined areas) which do not take into account the most fundamental aspect to be considered: the restriction and overlapping of endemic taxa, namely, the strict sympatry or homopatry, i.e. the presence of two or more distributional areas that completely overlap. Considering strictly sympatry, Escalante (2015) found that PAE performed better than the optimality criterion, although both methods may identify areas with some grade of sympatry. Also, although the optimality criterion identified more areas of endemism, their number of endemic

taxa strictly restricted was insufficient (at least two) to support some identified areas of endemism. Another problem is that results from the application of the optimality criterion are scale-dependent. Analyses using different cell sizes may recover different areas, all valid insofar as they all are supported by distributional congruence of species at that resolution or scale (Navarro et al. 2009; Szumik et al. 2012; Aagesen et al. 2013; Bertelli et al. 2017).

Analysis of Biotic Elements, Network Analysis Methods and Neighborjoining

Both PAE and the optimality criterion are based on an area pattern approach. Hausdorf and Hennig (2003) proposed an alternative approach that use biotic elements, i.e. groups of taxa whose ranges are significantly more similar to each other than those of taxa of other such groups (see Fattorini 2017). Hausdorf and Hennig's method consists of two steps. The first step in the analysis is to test the hypothesis that the observed degree of clustering of species ranges can be explained by the varying number of taxa per cell and the spatial autocorrelation of the occurrences of a taxon alone.

This test is based on Kulczynski 2 distances between the ranges of the examined taxa. A significant clustering of ranges means that the distances are small between ranges of the same cluster, while the distances between ranges of distinct clusters are large. The distribution of the test statistics under the null hypothesis of homogeneity is approximated by Monte Carlo generation of sets of ranges. Only if the analysed distribution areas are clustered, it is meaningful to determine biotic elements, which is the second step of the analysis. To identify biotic elements, the Kulczynski dissimilarity matrix between pairs of species is reduced using a non-metric multidimensional scaling. Then, a model-based Gaussian clustering is applied to establish the number of meaningful clusters and which ranges cannot be assigned adequately to any biotic elements (noise component).

After biotic elements are identified, their distribution can be mapped and areas where more than a prefixed percentage (e.g., >70%, >30%, and >0%) of the species of an element are present can be visualized. These areas can be considered as areas of endemism.

From a theoretical point of view, this approach has been criticized by Casagranda et al. (2012), because Kulczynski distances between species with identical ranges of distribution would follow a Gaussian distribution with variance zero, which would make paradoxically impossible to identify a perfect case of the pattern that the method intends to describe.

The analysis of biotic elements is very sensitive to the degree of congruence among the distributions of the species that define an area, with counter-intuitive results: the method often groups species with completely allopatric distributions in a single biotic element, fails to recognize biotic elements defined by perfectly sympatric species and its performance improves with increasing levels of noise in the species distributions (Casagranda et al. 2012).

Also, Dos Santos et al. (2008) noted that Kulkczinsky distance is misleading because it favours the inclusion of widespread species into biotic elements, clustering them with species of smaller ranges. To find patterns of sympatry, Dos Santos et al. (2008) proposed a different approach based on network analysis. Their approach consists of two parts. The first part is aimed at constructing a basal sympatry network based on punctual data, independent of a priori determination of areas. In this way, two or more species are considered sympatric when there is interpenetration and relative proximity among their records of occurrence. Groups of species presenting within-group sympatry and between-group allopatry constitute allopatric units of co-occurrence, which are however usually connected by intermediary species. The second part is a network analysis based on the identification and removal of intermediary species to segregate units of co-occurrence, using a betweenness measure and a clustering coefficient. The species ranges of the units of co-occurrence obtained are transferred to a map, being considered as candidates to areas of endemism. An important characteristic of this approach is that it is independent of predefined spatial units, but is based on georeferenced distributional records.

Another, recent method that does not require an a priori area determination is the Geographical Interpolation of Endemism (GIE), based on kernel spatial interpolation, proposed by Oliveira et al. (2015). GIE is based on the quantification of the co-occurrence of species,

weighted by the distance between the points of distribution records. Namely, this approach is based on estimating the overlap between the distribution of species through a kernel interpolation of centroids of species distribution and areas of influence defined from the distance between the centroid and the farthest point of occurrence of each species. GIE does not depend on grid cells, it allows the use of occurrence data with gaps, delimits areas of endemism with fuzzy edges, and displays directly on the map smaller areas of endemism contained in more inclusive areas of endemism.

Results from the analysis of sympatry networks may be roughly consistent with those obtained from PAE and optimality criterion. Differently from PAE, however, this approach does not produce a hierarchical arrangement, but groups of allopatric units. Areas recovered by the analysis of sympatry networks are supported by strictly endemic species that are not supporting elements elsewhere, whereas different combinations of cells in Szumik et al.'s (2002) results share many of their supporting species. Thus, differently from the endemicity analysis of Szumik et al.'s (2002), areas of endemism recovered with this approach are identified by a unique pool of supporting species.

However, Casagranda et al. (2009) noted that the interpenetration criteria of Dos Santos et al.'s (2008) approach can show erroneous sympatric relationships, and the betweenness criterion can have limitations in recognizing areas of endemism. Recently, dos Santos et al. (2012) proposed an improved approach of their network analysis based on weighted inference and the dynamic exploration of sympatry networks by using the cohesiveness criteria to reduce the betweenness bias.

A further development of the use of network analysis to identify areas of endemism has been recently prosed by Torres-Miarnad et al. (2013), with a network analysis method (NAM) which incorporates measures of the strength of the ties within the internal networks and uses an iterative procedure that increases the number of possible areas of endemism by minimizing the effect of minimal overlap. Torres-Miarnad et al. (2013) also proposed the use of neighborjoining (NJ) to reflect the idea that areas diverge among themselves in a differential way, with long branches corresponding to zones with high speciation rates and complex histories (biotic and tectonic), and short branches corresponding to zones with low speciation rates and simple histories. According to Torres-Miarnad et al. (2013), the NJ method has advantages over the other tree-like methods (such as PAE), because it can identify complex areas through a minimal evolution principle, maximizing the weight of those species that have wide distributions, and thus offering major inclusion relationships.

In a study comparing PAE, optimality criterion and GIE (Oliveira et al. 2015), results obtained by PAE and GIE differed mainly in the shape of the areas of endemism and the number of endemic species identified in each area, while NDM results were relatively similar to those from GIE, but GIE allowed a finer resolution. All these methods are promising, but more empirical studies are needed to assess their pros and cons.

Range-Size Rarity and Weighted Endemism

The aforementioned methods attempt to identify areas of endemism on the basis of species occurrence without any explicit measure of the extent of their ranges, i.e. their range-size (although species with different distribution contribute in a different way to the outcomes). However, incorporating the concept of geographical rarity in area prioritization is of key importance in biological conservation, because species with small ranges may also have small population sizes, which increases their extinction risk.

Definitions of endemism based on threshold values of absolute or relative range size or restriction (Rosauer et al. 2009) may be useful in some circumstances (Mokany et al. 2014), but they are somewhat arbitrary (Crisp et al. 2001, Kier and Barthlott 2001, Laffan and Crisp 2003). For example, Terborgh and Winter (1983) and Gentry (1986) suggested a fixed threshold value of 50,000 km^2 for defining endemism of birds and plants, but this is inappropriate for many taxa where the majority of species has ranges well below this threshold value. Because range sizes are known to differ among taxa (Gaston 1994, Gaston and Williams 1996), Gaston (1994) suggested using the lower quartile of range sizes of species of a given higher taxon as the limit between endemic and widespread species. However, this definition is dependent on the selection of species considered in the analysis. Thus, a given species may be classified as 'endemic' in one data set and 'widespread' in another. For this reason, the use of threshold values

has increasingly superseded by methods that weight metrics of endemism by the range sizes of the taxa, rather than counting occurrences of species that meet a priori defined criteria.

If species distributions are represented using a grid system, endemism, expressed as a range-size rarity (*RSR*), can be calculated by counting the number of quadrats in which each species occurs, taking its inverse, and summing the total for each quadrat, as follows (Kerr 1997, Lovett et al. 2000, La Ferla et al. 2002):

$$RSR = \Sigma(1/C_j) \quad \text{(eq. 4)}$$

where C_j is the number of grid cells in which the species j was found. The maps of range size rarity are equivalent to measures of narrow endemism because endemism is the condition of being restricted to a particular area with a prescribed extent. Other authors used a different approach and calculated range-size rarity as the mean of the inverse value of the number of squares occupied by the range of all species recorded at a given site (Williams and Humphries 1994, Fjeldså et al. 1999, Kessler 2002). The skewed distribution of inverse range sizes implies that when taking the mean, species with very small ranges influence the score more strongly than do widespread species (Kessler 2002).

Taking the inverse of species ranges to express endemism is a form of weighting, and for this reason the *RSR* it is known as a form weighted endemism (*WE*). Weighting functions can be of any shape, and those used in literature include inverse of range weighting (as described above) and Gaussian forms (Laffan and Crisp 2003). Because cells with a large number of species are expected to contain a large number of endemics by change alone, WE values tend to be positively correlated with species richness. For this reason, Crisp et al. (2001) proposed to divide the *WE* score by the species richness of a cell (Corrected Weighted Endemism, *CWE*). However, an important limit of this approach is that it does not consider how species are spatially aggregated, because each cell is considered independently. To surpass this problem, Laffan and Crisp et al. (2003) introduced the Spatial Corrected Weighted Endemism (Spatial *CWE*). The Spatial *CWE* is calculated as follows. First, for each cell a weighted endemism (*WE*) score is calculated as the sum of the ratios between the number of times a species occurs in a predefined local neighbourhood, rather than only in the central cell, and the total number of cells from which the species has been recorded. Then, the *WE* score is divided by the number of species occurring in the central cell to correct for species richness. For example, consider a cell and its four immediate North, East, South and West neighbours. Let us presume the existence of three species in the central cell. One of the species occurs in three of the five grids in our sample area and in four grids in total (one outside the neighbourhood), thus showing a very restricted distribution. The second species is more widely distributed, with two of 20 and the third species is very widespread with four of 1000. The calculation of the *CWE* for this grid cell is $CWE = (3/4 + 2/20 + 4/1000)/3 = 0.285$.

Progressive extension of the neighbourhood to larger spatial extents allows an understanding of how the endemism of species in the central cell changes with increasing spatial scale. For example, in their study of the Australian vascular flora, Laffan and Crisp et al. (2003) considered no neighbours, one-cell radius neighbours (i.e. the focal cell and four neighbouring cells), two-cell radius neighbours (i.e. the focal cell and 12 neighbouring cells), and three-cell radius neighbours (i.e. the focal cell and 28 neighbouring cells). Recently, the weighted endemism approach was further developed by Guerin et al. (2015) using georeferenced range estimates.

The value of weighted endemism for each grid cell obtained with these methods depends on the species composition and total number of grid cells. Thus, any change in the species distributional data will change the values of many or all grid cells, which makes these methods very sensitive to the quality of distributional information.

Phylogenetic Measurements of Endemism (PE)

In ecological research, phylogenetic relationships are usually treated more as a "problem" that should be controlled for due to the non independence of data because of phylogenetic autocorrelation (Felsenstein 1985, Strona et al. 2012) than a possible source of diversity, and the role of phylogeny as a driving factor of macroecological patterns has only recently come into focus (Harcourt et al. 2005).

From a conservation point of view, it might be useful to evaluate the degree of phylogenetic diversity that an area hosts. The term phylogenetic diversity (*PD*) was introduced by Faith (1992) and represents the sum of the branch lengths of a phylogenetic tree. *PD* in a given area is higher if there are many old taxa, lower if the taxa are younger and/or if the number of taxa is smaller. Using the values of *PD* of the taxa occurring in a given area it is thus possible to calculate a phylogenetic measure of endemism. Faith et al. (2004) defined *PD* endemism as the amount of *PD* entirely restricted to a given area – a phylogenetic measure of absolute endemism. Equivalent measures had been used previously by Sechrest et al. (2002) and by Mooers and Atkins (2003). An important limit of studies based on absolute endemism (e.g., Sechrest et al. 2002, Mooers and Atkins 2003, Faith et al. 2004, Spathelf and Waite 2007) is that they detect endemism only where the spatial unit of measurement encompasses the entire ranges of the concerned taxa. Thus, one must choose between coarse spatial units that can show only very broad patterns, and smaller spatial units that detect only the narrowest range endemism. To surpass this problem, Rosauer et al. (2009) proposed a phylogenetic form of weighted endemism (called phylogenetic endemism, *PE*) which makes it possible to map endemism at a finer spatial grain while being sensitive to range restriction at coarser scales.

PE is the sum of branch length/clade range for each branch on the spanning path linking a set of taxa to the root of the tree:

$$PE = \sum_{[c \in C]} \frac{L_c}{R_c} \qquad \text{(eq. 5)}$$

where:

L_c is the length of branch c (expressed here as proportion of the total length of the tree);

R_c is the clade range, i.e. the union of the combined ranges of the taxa descended on the phylogeny from branch c, such that overlapping areas are considered only once;

c is a branch (a single segment between two nodes) in the set of branches in the minimum spanning path joining the taxa to the root of the tree.

PE is high if a small region captures a large fraction of a clade's evolutionary diversity, lower if the region is larger or if the fraction is smaller (Cadotte and Davies 2010, Rosauer et al. 2009).

Tucker et al. (2012) used a similar approach based on the "biogeographically weighted evolutionary distinctiveness (*BED*)". *BED* values scale evolutionary distinctiveness values by species' range sizes. When *BED* is summed for all species in a site, this represents the total biogeographically weighted evolutionary distinctiveness (*BEDT*).

BED is calculated as:

$$BED(T,i) = \sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e} \qquad \text{(eq. 6)}$$

where n_e is the number of grid cells in which a species is present, below branch e, in the set $q(T,i,r)$, which includes the branches connecting species i to the root r of tree T, and λ is the length of the branch e. The metric *BEDT* is then the summation of the *BED* values of all species in a site; thus, sites with species that are narrowly distributed will have higher *BEDT* than sites with widely distributed species.

ENDEMISM AND HOTSPOTS

The concept of biodiversity hotspots

The concept of biodiversity hotspots, as coined by Myers (1988, 1990), refers to areas that host a large number of endemic species and that are, at the same time, under severe threats. According to hotspot definitions given by Myers (1988, 1990), Mittermeier et al. (1999, 2005) and Myers et al. (2000), to qualify as a biodiversity hotspot, a region must have a high percentage of endemic species (namely vascular plants) and 30% or less of its original natural vegetation. However, since its introduction, the concept of biodiversity hotspots has been defined in many other ways, for example as areas with high numbers of species (e.g., Prendergast et al. 1993, Myers et al. 2000, Veech 2000, Brummitt and Nic Lughadha 2003, Maes et al. 2003, Ovadia 2003), rare and threatened taxa (Dobson et al. 1997; Troumbis and Dimitrakopoulos 1998; Griffin 1999; Possingham and Wilson, 2005, Funk and Fa, 2010), endemic species (e.g., Lumaret and Lobo 1996), or a combination of richness and endemism (e.g., Kier and Barthlott 2001; Hobohm 2003). The panbiogeographical concept of a node (i.e. the intersection of two or more generalized

tracks) may be thought of as equivalent to a biodiversity hotspot (Craw et al. 1999).

Proportion of Endemics (E/S)

The percentage of taxa endemic to an area (i.e. the proportion of endemic species, *E*, to the total number of species, *S*, living a given area) is the most frequently used measure to characterize the relative endemism of the biota of that area (see Anderson 1994) and to compare the number of species with size of the area (see Fattorini 2007b) for hotspot identification.

However, the use of percentages is problematic for two important reasons. First, percentages obscure differences in raw numbers that can be important in conservation biology (Magurran and McGill 2011, Ungricht 2004, Hobohm 2000). The same percent value can be obtained by completely different values of *E* and *S*. Thus, an area with a total of 10 species, 5 of which endemic, will have the same percentage of endemics as an area with 100 species, 50 of which endemic, but the importance of the two areas will be very different if we also value species richness. Second, if the number of endemic species is correlated with the number of non-endemic species, the percentage of endemic species among all species recorded in a given area is not an unbiased measure of the level of endemism. This problem has been stressed by Vilenkin and Chikatunov (1998; hereafter V&C) in terms of a regression approach. If *E* is the number of endemics (i.e. the species occurring only within the limits of a well defined area), and *NE* is the number of non-endemics (i.e. all species with ranges extending outside the focal area), the percentage of endemism is:

$$\%E = 100 \times E/(E + NE) \quad \text{(eq. 7)}$$

hence

$$E = NE \times \%E/(100 - \%E) \quad \text{(eq. 8)}$$

V&C noted that when the separate faunas in a series of areas are the focus of interest, the term $\%E/(100 - \%E) = b$ can be considered as the regression coefficient of *E* on *NE*.

If the regression of the number of *E* on *NE* is not significant, the *E* and *NE* numbers are statistically independent and *%E*, the endemism percentage, is a sufficient characteristic of the endemism level in each particular fauna. By contrast, a significant regression indicates a certain trend in endemism values and, according to this trend, mean endemism percentage

$$\%E = 100 \times b/(b + 1) \quad \text{(eq. 9)}$$

The *%E* value in such a case is independent of the total species number, and the endemism level of each particular fauna may be evaluated as the observed percentage deviation from the expected value (the value predicted by the equation). *%E* will also depend on the total species number if the intercept in the regression of *E* on *NE* (or vice versa) is not zero. In all such cases, according to V&C, the endemism percentage is not an adequate measurement of the comparative distinctiveness of the local fauna under consideration, and residuals from regression should be used as they are more appropriate measures.

V&C developed several distinct procedures for analysing the relationships between endemic species and species belonging to other biogeographical ranks. To calculate the values of endemic species expected on the basis of possible relationships with species belonging to other biogeographical ranks, V&C used the following model:

$$\ln(E + 1) = a + bNE \quad \text{(eq. 10)}$$

where *a* and *b* are fitted parameters (see also Vilenkin and Chikatunov 2000, Vilenkin et al. 2009). This equation allows the investigator to assess if the number of endemic species is influenced by the number of non-endemics.

The expected values according to calculations can be compared with the observed values and the residuals can be used as an estimation of level of endemism. Areas are then ranked according to the magnitude of residuals and according to the simple percentage of endemic species. If the two methods agree, the number of endemic species is not influenced by the number of regional (non-endemic) species. If the two methods give different arrangements of islands, the number of endemic species is influenced by the number of regional species.

An empirical analysis conducted on the tenebrionids of the Aegean Islands (Fattorini, 2007b) revealed that, as hypothesized by V&C, the number of endemic taxa was influenced by both the number of taxa of other biogeographical ranks, and by an island's area. However, explanations for the

positive relationship between the number of endemic taxa and taxa of different biogeographical ranks are equivocal. Also, this relationship did not necessarily influence the level of endemism, which could be expressed adequately by percentages.

The use of *E/S* ratios (or percentages) may be justified to compensate for differences in area size. Larger areas tend to have more species and hence more endemics. Thus, a certain region may appear poorer in endemics only because of smaller size in comparison with other regions. However, because the species-area relationship (SAR) is not necessarily linear, dividing by *S* cannot be appropriate to take into account differences in area size.

Some authors suggested to compare regions of different areas by using the density of endemics, calculated as the number of endemics (*E*) over area (*A*). The number of endemic species divided by area may be appropriate for areas of similar sizes, but can be misleading for regions with different area sizes, because the number of endemics does not necessarily increase linearly with area. Because endemics are a subset of the total species richness, this is exactly the same type of mistake that occurs when using species-area ratios. Some authors used species-area ratios in hotspot identification (e.g., Mittermeier et al. 1998, Myers et al. 2000), but it would be correct only if species increase linearly with area. However, SAR is not necessarily linear, so one cannot divide the total species richness by the area and report the result as species per unit area (e.g., Veech 2000, Brummitt and Nic Lughadha 2003, Ovadia 2003).

Although several mathematical functions have been proposed to model SARs (Tjørve 2003, 2009, Dengler 2009, Williams et al. 2009), comparative studies identify the power function,

$$S = CA^z \qquad \text{(eq. 11)}$$

where *S* represents species richness, *A* the area, and *C* and *z* are fitted parameters, as the model that, in general, best fits empirical data (Triantis et al. 2012, Matthews et al. 2015), and which is best supported by ecological theories (e.g., Rosenzweig 1995, Martin and Goldenfeld 2006).

Assuming the power function as the best model, Ovadia (2003) and Brummitt and Nic Lughadha (2003) proposed the use of the *C* parameter as a measure of species richness standardized by area. Because *C* is the ratio of diversity (*S*) to A^z, the higher the *C* value the faster the increase in species richness, and consequently the higher the qualitative rank for the area. To obtain realistic scores of relative diversity, it is however important to use appropriate values of *z*. For example, Ovadia (2003) and Brummitt and Nic Lughadha (2003) used a priori *z* values such as 0.14, 0.18, and 0.25, but since *z* varies according to the study system, appropriate choices should be made on the basis of empirical evaluations (Fattorini 2006). Of course, the simple *S/A* ratio would be appropriate only if $z = 1$. The power function model for SAR can reformulated for the analysis of the endemics as

$$E=CA^z \qquad \text{(eq. 12)}$$

and hence the *E/A* ratio would be appropriate only if $z = 1$. In fact, it seems that, after some statistical adjustment, species-area relationships modelled for the endemics alone, i.e. the endemics-area relationships (EARs), tend to have *z*-values close to one (Storch et al. 2012).

Of course, the impact of the non-linearity of the EAR is large when the compared regions have very different areas, whereas it is negligible for regions with similar size, because for small differences in area size the curvilinear shape of the EAR can be well approximated by a straight line. Thus, the *E/A* is an appropriate measure of endemism density for areas of similar sizes. However, if the compared regions are approximately of the same size, then we can compare absolute numbers of endemics (*E*) directly, and there is no need to standardize for *A*. Similarly, it is possible to compare directly regions that have different areas but very similar numbers of endemics. In this case, the region with the smaller area is that with the highest concentration (density) of endemics (Hobohm and Tucker 2014).

Endemics-Area Relationships (EARs)

In a nested plot design, where every small plot is included in a larger one, the *z*-value of the EAR should be as high or higher than 1, because the number of endemics should increase at the same rate or more rapidly than the total number of species. This was empirically confirmed by Storch et al. (2012), who found that the EARs for amphibians, birds and mammals at global scale can

be assimilated into one universal power law with a z-value close to 1 after the area is rescaled by using the range sizes of the taxa.

However, the situation is very different for dispersed and independent areas, such as islands or regions, where the largest areas are not the sum of the smaller ones. In these cases, the z values are much more variable and often lower than 1 (cf. Georghiou and Delipetrou 2010, Werner and Buszko 2005, Hobohm 2000, Triantis et al. 2008). This makes it difficult the use of the C values to compare the levels of endemicity for different taxa in the same system (e.g., different taxa in the same archipelago) or for the same taxon in different systems (e.g., the same taxon in different archipelagos). In fact, neither the C value nor the z value represents the magnitude of species diversity, because both parameters are responsible for the shape of the function, and C values can be compared only when z values are similar. This problem can be easily understood if reformulated in terms of ANCOVAs, where intercepts can be compared only for parallel regression lines, i.e. for lines with similar slopes. The power function can be linearized with a double logarithmic transformation, which allows the application of regression analyses. The linearized versions for the SAR and the EAR are

$$\log S = \log C + z\log A \qquad \text{(eq. 13)}$$

and

$$\log E = \log C + z\log A \qquad \text{(eq. 14)}$$

respectively. When fitting these lines by regression procedures, C and z are unrelated, in the sense that they are estimated independently and jointly describe the data: z can be interpreted as a scaling factor describing how fast the response of species richness to area changes along the curve, while C represents the expected mean number of species, or endemic species, per unit area (Fattorini et al. 2017). Nevertheless, in the log–log space, when z increases, the fitting line tends to be more vertical, and hence it has more chances to intercept the y-axis at lower values. Consequently, systems with higher z values tend, on average, to have lower C values. For this reason, C values should be compared only in families of regression lines having the same slopes (i.e. between parallel lines) (Gould 1979, Fattorini et al. 2017). If EARs have similar slopes, as observed in the nested plot designs, C can be the correct measure of endemic diversity per unit area; but if z are different, as frequently observed in the case of independent area designs, comparing C values may be misleading.

In considering the dependence of species number on area, Vilenkin and Chikatunov (1998, hereafter V&C) adopted linear or second-power approximations to develop formulae to calculate the expected number of endemic species by area without providing any biological justification for such a procedure. When selecting a polynomial approximation, they used $A^{0.5}$ because area is already to the second power.

The resulting equations were:

$$E = a + b\,A^{0.5} + cA \qquad \text{(eq. 15)}$$

and

$$E = a + b\,A^{0.5} + cA + dNE \qquad \text{(eq. 16)}$$

The last equation also considers the possible contribution of non-endemic species (NE). This equation is not reported by V&C who, in contrast, presented the model:

$$E = b\,A^{0.5} + dNE \qquad \text{(eq. 17)}$$

but it was given by Fattorini (2007b) as a submodel of equation 16, where a and cA did not appear because they were not statistically significant for V&C's data. To prioritize areas, expected values according to calculations can compared with the observed values, and the residuals used as an estimation of level of endemism. Apart from the empirical analysis reported in Fattorini (2007b), these models remain however unexplored.

Use of SARs and EARs to forecast species extinction

The power-function of the SAR has been repeatedly used to predict species extinction with habitat reduction (e.g., Reid and Miller 1989, Wilson 1992, Ney-Nifle and Mangel 2000, Wilsey et al. 2005, May et al. 1995, Rosenzweig 1995, Triantis et al. 2010). If we suppose a reduction of area A_0 to A_1, so that the number of species S_0 is expected to decline to S_1, we obtain, after rearrangements

$$S_1 = S_0 \times (A_1/A_0)^z \qquad \text{(eq. 18)}$$

The term $(A_1/A_0)^z$ thus represents the proportion of remaining species after area reduction.

Harte and Kinzig (1997) and Kinzig and Harte (2000) argued that the use of SARs tends to

overestimate real species loss after small to moderate habitat loss. To correct for this, they assumed that an area is subsequently subdivided into smaller parts and that in each part the original allometric species–area relation (e.q. 11) should be applied. This assumption refers in particular to a situation where species have similar scale invariant spatial distribution patterns (Harte et al. 1999). Kinzig and Harte (2000) also argued that EARs and SARs can be both modelled using the power function, but EARs provide more reliable estimates of species loss during a process of habitat destruction. Namely, Kinzig and Harte (2000) have showed that using the appropriate EARs, recent rates of species loss may underestimate future species extinctions under continued land clearing, but some results are controversial (see e.g., Pereira and Daily 2006). However, He and Hubbell (2011) have recently identified some important theoretical flaws in the statistical assumptions on which the method is based, and claimed that the function that relates species loss with decreasing habitat area cannot be obtained simply by reversing the species-area accumulation curve.

EARs are commonly believed to have much higher slopes than the underlying SARs (Harte and Kinzig 1997; Harte 2000; Kinzig and Harte 2000; Ulrich and Buszko 2003a). However, He and Hubbell (2011) found that the z values of the EARs tend to be much lower (typically half) than those of the respective SARs and therefore they concluded that SARs always overestimate extinction rates from habitat loss. However, they based this conclusion mostly on theoretical reasoning, with a few examples from the real world (Brooks et al. 2011, Evans et al. 2011).

According to Brooks (2011), He and Hubbell (2011) assumptions are wrong, because species that seem to persist in the remaining fragments are condemned to extinction, if fragments are too small, whereas Pereira et al. (2012) noted that He and Hubbell's conclusions are not general but depend on the geometry of habitat destruction and the scale of the SAR (but see He and Hubbell 2012).

Ulrich (2005) used a patch occupancy approach for studying EARs and SARs with simulated communities. This approach has the advantage of allowing the generation and analysis of multiple replicable spatial distribution patterns with sample areas that have the same spatial properties as those that were assumed for the theoretical derivations of SARs and EARs. He concluded that the EAR approach proposed by Harte and Kinzig (1997) and Kinzig and Harte (2000) for estimating species loss during habitat destruction does not give better results than the use of classical SARs. Ulrich (2005) also compared SAR and EAR results obtained for butterflies of European countries and found that the goodness of fit of the models might influence the applicability of EARs more than that of SARs. Moreover, Ulrich and Buszko (2005) showed that for the European butterflies the use of SARs and EARs lead to different predictions about diversity loss and prioritizing schemes for conservation. More in general, Ulrich (2005) noted that SARs have low goodness of fit values, which makes even moderate extrapolations beyond the range of measurements (and hence estimates of extinctions) doubtful, especially due to the large confidence ranges for species numbers at small and large area scales.

Apart from theoretical debates, surprisingly few papers investigated the applicability of SARs (May et al. 1995, Pimm and Askins 1995, Pimm 1998, Ulrich and Buszko 2003a, b) for predicting species loss. However, empirical evidence indicates that SARs do not necessarily overestimate, but typically underestimate extinction rates (Fattorini and Borges 2012).

Use of SARs and EARs for the identification of hotspots

Some authors (e.g., Veech 2000, Ulrich and Buszko 2005, Fattorini 2006) propose to use the SAR (or the EAR) for hotspots identification. In practice, after the SAR is fitted, the areas displaced above the fitting curve (i.e. those having a positive residual) are considered as hotspots because these areas have more species than predicted by the fitting function.

Although the power-function provides the best fit in most cases, the hotspots revealed by a particular curve-fitting function could be different if the same data are fitted with a different function. Thus, Veech (2000) proposed applying various fitting functions and considering as hotspots the areas with higher positive residuals in most models.

Hobohm (2003) introduced an index defined as:

$$\alpha = \log S - (z\log A + \log C) \qquad \text{(eq. 19)}$$

It can be demonstrated that the α value of a given area is exactly its residual from the linearized power function regression line. Thus, this method is exactly the same as using residuals.

This approach, is, however, problematic. The use of residuals may lead to areas being identified as hotspots if they have higher species richness than predicted by the best-fit model for almost every size class of richness and can be produce misleading results when applied to EARs including areas with zero endemics (Fattorini 2006). In this circumstance, the importance of endemics should be evaluated according to different methods, such as percentages, to take into account different levels of endemism and different kinds of endemic species (e.g., endemic to single islands vs. endemic to the archipelago). Of course, hotspots based on SARs or EARs include a fraction of the overall diversity, and one should ask how representative this fraction is. In fact, the ability of hotspots based on SARs or EARs to conserve total species diversity has been questioned (Fagan and Kareiva 1997, Kerr 1997, Pimm and Lawton 1998, Reid 1998, Andelman and Fagan 2000) and the use of EARs or SARs based on threatened species only does not seem to improve the outcome (Bonn et al. 2002).

CONCLUSIONS

Among the methods used to identify areas of endemism, the optimality criterion seems to be more efficient than the Parsimony Analysis of Endemism (PAE), although PAE may be useful to disclose hierarchical relationships. PAE remains the best explored method and may represent a useful benchmark for testing other methods. Recently proposed approaches, such as the analysis of nested areas of endemism, networks and neighborjoining, are promising, but need to be more widely tested. All these methods attempt to identify biogeographically homogeneous sets of areas characterized by shared species, without any attempt to evaluate their relative importance for conservation purposes. Analyses based on weighted endemism methods identify areas of endemism according to specie distributional rarity and phylogenetic position, being thus appropriate for conservation purposes.

The proportion of endemic species to he total number of species living a given area is the most frequently used measure to rank areas according to their relative endemism. However, proportions obscure differences in raw numbers that can be important in conservation biology. Because the number of (endemic) species tends to increase with area, some authors proposed to model the endemics-area relationship and to consider the areas displaced above the fitting curve (i.e. those having a positive residual) as hotspots. However, the use of residuals may lead to areas being identified as hotspots for almost every size class of richness. Thus, it is important to evaluate the ability of the hotspots recovered by these procedures to really conserve total and endemic species diversity.

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