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6 **A history of chorological categories**

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18 **Abstract** One of the purposes of the research program referred to as “systematic biogeography” is the
19 use of species distributions to identify regions and reconstruct biotic area relationships. The reverse, i.e.
20 to group species according to the areas that they live in, leads to the recognition of chorological
21 categories. Biogeographers, working under these two different approaches, have proposed several terms
22 to refer to groups of species that have similar distributions, such as “element”, “chorotype” and
23 “component”. A historical reconstruction, including semantic observations and philosophical
24 implications, shows that these terms have been used in a variety of senses. The word “component” should
25 not be used in biogeography. The word “element” has been used to identify both a group of species
26 defined according to the biogeographic areas they occupy and a group of species with an assumed shared
27 biogeographic history. It is especially because of the influence of the dispersalist paradigm, which
28 dominated evolutionary thought until the mid-twentieth century, that the second definition has been
29 frequently adopted. The term “element” is therefore ambiguous and its use should always be associated
30 with an explicit definition. The word “chorotype” should be used to define groups of species with similar
31 ranges when no causal assumption is made. The concept of “chorotype,” finally, should not be
32 confounded with other concepts such as distributional pattern, cenocron, horofauna, biota, endemic area,
33 area of endemism, biotic element, and generalized track, which are also discussed in this paper.

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36 **Key words:** Biogeography – Chorological categories – Chorotype – Component – Element.

37 **Introduction**

38

39 Biogeography is the “study of the distribution, and of the patterns of distribution, of living organisms at
40 all levels” (Cox and Moore 2010, p. 475). While biogeography can be defined by its object (distribution),
41 it nevertheless does not approach this object in one way only. Biogeography is a multidisciplinary science
42 with many, sometimes very different, but usually complementary research programmes and many authors
43 attempted to divide it into sub-disciplines on the basis of subjects, methods and aims.

44 For example, De Lattin (1967) and Müller (1974) divided zoogeography (but the same can be applied to
45 biogeography in general) into descriptive and causal sub-disciplines. Following Müller, descriptive
46 zoogeography attempts to describe and organize the diversity of “living phenomena in space.” Causal
47 zoogeography, on the other hand, can be further divided into ecological and historical zoogeography.
48 Ecological zoogeography investigates the ecological relationships between the species and the
49 environmental characteristics of the places they occupy. Historical zoogeography tries to explain current
50 distributions taking into account phylogeny and earth history. In the last decades, differences in
51 epistemological premises and methodological approaches have led to a split of historical biogeography
52 into a number of further sub-disciplines, such as panbiogeography, vicariance biogeography and
53 phylogeography (Crisci *et al.* 2003). Several authors have criticized the lack of interaction between
54 historical and ecological biogeography and some have called for an integration of them into a unified
55 research program (see Morrone 2009).

56 From a more conceptual point of view, Parenti and Ebach distinguished between “systematic
57 biogeography,” which consists in the study of biotic area relationships and their classification, and
58 “evolutionary biogeography,” which consists in the proposal of evolutionary mechanisms responsible for
59 organismal distributions. They also propose to unify these two types of biogeographic investigation into a
60 comprehensive research program they called “comparative biogeography” (Parenti and Ebach 2009, p. 9;
61 see also Ebach and Goujet 2006).¹

62 In the framework of “descriptive biogeography”, most work has been done in terms of using species
63 distributions to identify regions characterized by particular species assemblages.² The first known
64 example of an explicit biogeographic regionalization is Lamarck and de Candolle's (1805) subdivision of
65 France into regions based on plant distribution (Ebach and Goujet 2006). Celebrated early examples of

¹ The expression “systematic biogeography” has also been used in a somewhat more restricted way to indicate the study of area homologues (statements of relationship among three or more biotic areas) and area homologies (the patterns “expressed” by area homologues); see Williams and Ebach (2008).

² This form of regionalization is based on taxic distribution and should not be confused with other forms of regionalization based on plant growth forms and types of vegetation, first introduced by von Humboldt (von Humboldt and Bonpland 1829; see Ebach 2015 for a discussion). Concepts such as those of elevational belts, latitudinal belts, biomes, life zones and biotic provinces (see Udvardy 1969 for a historical discussion) can be considered as derivatives of von Humboldt's approach. Whereas regionalizations based on taxic distributions are heavily reliant on systematics and taxonomy, von Humboldt's approach is based on eco-morphological criteria. Although Udvardy (1969) introduced the word “faunation” as a zoological counterpart of “vegetation”, it remained substantially ignored by zoogeographers.

66 biogeographic regionalizations at a global scale are, among others, de Candolle's (1820) botanical
67 regions, Prichard's (1826) and Schmarda's (1853) zoological regions, and Sclater's (1858) ornithological
68 regions (see Parenti and Ebach 2009, p. 21-27; Ebach 2015, pp. 37, 113-136). Regionalization as a
69 biogeographic research program is still flourishing (Ebach and Parenti 2015), as shown, for example, by
70 a recent update of Wallace's zoogeographical regions (e.g., Holt *et al.* 2013). Recognition of areas of
71 endemism can be also considered a particular approach to regionalization, although there are many,
72 partially contrasting definitions of areas of endemism (reviewed in Parenti and Ebach 2009 and Morrone
73 2014) and procedures for their identification (see Parenti and Ebach 2009).³
74 Regionalization is a form of classification and thus belongs to the biogeographic research program
75 referred to as "systematic biogeography" (see above). Regionalization studies (including the
76 identification of areas of endemism) use species distributions to divide the geographical space into units,
77 and then proceed by a form of descriptive research within the broader biogeographic scope of biotic area
78 relationships. In these studies, areas are recognized, grouped and divided on the basis of the species that
79 they share. However, the reverse is also possible, i.e. to group species according to the areas where they
80 live. Like the study of species-area relationships, species grouping has also a long tradition in the history
81 of biogeography and practicing biogeographers largely use such species groupings, although typically in
82 a loose way. Species ranges are frequently used as fundamental units by practitioners of biogeography
83 and most work has been carried out, at the descriptive level, in order to study geographical distributions
84 by analytic and synthetic methods under the rubric of "areography" (Udvardy 1969; but see Rapoport
85 1982 for a different use of this word). Quite surprisingly, however, this research program has received
86 much less attention by theoreticians and historians of science.
87 Comparative analyses of species ranges may be used for different purposes and then can produce very
88 different systems of biogeographic classification. Whereas regionalization systems produce hierarchical
89 classifications (e.g., realms, regions, dominions, provinces and districts; Morrone 2009), which can be
90 expressed by formal taxonomic arrangements subject to nomenclatorial rules (see Ebach *et al.* 2008),
91 areographic recognition of species groupings based on recurrent, similar species ranges is not used to
92 produce hierarchical classifications, but as a tool for biogeographic analysis. This fundamental difference
93 is inherent to the different properties of the objects that are classified. In the case of regionalization, what
94 is classified are areas. Although there is no agreement in area definition and identification (Parenti and
95 Ebach 2009), areas are always treated as non-overlapping entities, with the possible exception of areas
96 that show "transitional" features. This makes the treatment of areas in biogeographic regionalization very
97 similar to that of species in biological systematics (Morrone 2009). Although both biologists and
98 philosophers disagree on the proper definition of the term "species" and its ontological status (e.g.,
99 Mayden 1997; Ereshefsky 2001, 2007), species are recognized by practitioners of biological systematics
100 as non overlapping units (at least under a synchronic viewpoint; see Schulz *et al.* 2008), with exceptions
101 due to hybridization processes.⁴ By contrast, because in any place more than one species occurs, species

³ Note that the term "endemic area" ("the geographical area to which a taxon or biota is understood to be native", Parenti and Ebach 2009, p. 253) refers to the distributional area of a taxon, so it is not equivalent to "area of endemism".

⁴ In analogy with hybridization between species, Morrone (2009) considers zones of biogeographic transition as events of biotic hybridization.

102 ranges are frequently overlapping, so they cannot be arranged into perfectly hierarchical classifications
103 similar to that used for species.

104 In order to better understand the distinction I am discussing here, it is useful to consider the concept of
105 hierarchy more generally. Two main hierarchies have been identified in nature: the genealogical
106 hierarchy and the ecological hierarchy (Eldredge 1985). The genealogical hierarchy consists of entities
107 named replicators, the ecological hierarchy includes entities named interactors. Organisms are the only
108 members that are common to both hierarchies. Accordingly, Morrone (2009) considered biotas as
109 interactors and clades as replicators. However, areas of endemism are both interactors and replicators,
110 because when the biota of an area is subject to a vicariance event, the two resulting biotas will inherit
111 some of the species of the former area. Actually, current biogeographic regionalizations assume that
112 natural areas should be recognized as monophyletic groups (Ebach and Parenti 2015) as expected for
113 replicators. At the same time, species are clades that interact within the areas they share. The problem
114 arises here whether a group of species that occupies a certain area should be considered a replicator or an
115 interactor. Comparative analyses of species ranges led to the proposal of a number of concepts that reflect
116 both possibilities. For example, Reig (1981) used the expression “distributional pattern” to indicate the
117 coincident form that the distributional areas of a set of monophyletic groups assume as a consequence of
118 a common biogeographic history, which implies that distributional patterns “evolve,” which is a property
119 of replicators. The same expression was also used by Halffter (1987, pp. 96-97) to indicate the “synthesis
120 of the essential features of the distribution of a set of coexisting organisms that originated or became
121 integrated in a given area and time, are subjected to the same macroecological pressures for a prolonged
122 period, live under the same physiographic conditions, and have a common biogeographic history”.

123 Note that Halffter adopted the expression “distributional pattern” to replace his former “dispersal pattern”
124 (Halffter 1962), to avoid any reference to the way a taxon reached a given distribution (i.e. by dispersal
125 or vicariance). A distributional pattern corresponds to the current distribution of a cenocron, a concept
126 introduced by Reig (1962, p. 131) to refer to a group of animal or plant species which, whatever their
127 origin, entered into a given area within a given geological timeframe. This concept was revised by
128 Morrone (2009, p. 18), who defined cenocrons as “sets of taxa that share the same biogeographic history,
129 constituting identifiable subsets within a biotic component by their common biotic origin and
130 evolutionary history.”⁵ Thus, when applied to animals, the concept of cenocron is very similar to that of
131 horofauna, a term coined by Smith (1949, p. 220) to refer to faunas of similar temporal and
132 zoogeographic origin, as opposed to faunas only based on similar location. Reig (1981, pp. 27-28)
133 distinguished his concept of cenocron from that of horofauna by defining the latter as an assemblage of
134 species that coexist and diversify in a given area during a prolonged time, thus representing a lasting
135 biogeographic unit. Thus, Reig’s use of horofauna can be considered an application to entire biotas of
136 Reig’s (1962, pp. 1981) and Morrone’s (2009) concepts of cenocron as well as Smith’s (1949) concept of
137 horofauna, all of which were used not for entire biotas, but for subsets within biotas (see Morrone 2014
138 for a discussion). Emphasizing a common phylogenetic or biogeographic origin of the taxa that form the

⁵ Morrone (2009) defines “biotic components” as “sets of spatiotemporally integrated taxa that coexist in given areas, representing biogeographic units, from a synchronic or proximal perspective”. According to Morrone (2009), both areas of endemism and Croizat’s generalized tracks (see below, section “What is a chorotype?”) represent biotic components.

139 assemblages identified by all of these concepts implies inheritance and hence that such assemblages are
140 replicators. In the following I will concentrate on concepts used to identify – on biogeographic grounds –
141 species groups that are interactors, but not necessarily replicators. In other words, I focus on
142 “chorological” groups that do not necessarily have a common phylogenetic or biogeographic origin.
143 Haeckel (1866, p. 287) coined the word “chorology” to refer to the study of the geographical and
144 topographical spread of organisms away from a centre of origin, and Ebach and Goujet (2006) use this
145 word to indicate the use of evolutionary models to trace distributional pathways. However, “chorology”
146 has been generally used in a more phenomenological sense (e.g. De Lattin 1967, Zunino and Zullini
147 1995) to indicate the study aimed at the identification of recurrent patterns, which are typically referred to
148 as “chorological categories”. This basic approach was first developed by botanists, such as Hooker and
149 Thomson (1855), Christ (1867) and Engler (1882). Since these pioneering studies, it has been clear that,
150 in the geography of floras, certain patterns of distribution frequently recur, bringing the plants they
151 represent into geographic relationships. Distributions that are centred in the same region and whose
152 boundaries broadly overlap can be grouped together and regarded as members of the same chorological
153 category. However, there is much confusion about concepts and terminology in the past and current
154 literature. In the following section, I focus on one particular source of confusion, the use of the terms
155 “element” and “chorotype”.

156

157

158 **Origin and use of the word “element” in biogeography**

159

160 The geographical categories used to group species with similar distributions have frequently been
161 referred to as “chorological elements”. In fact, the word “element” seems semantically not very
162 appropriate to express the idea of a group, since elements are the single objects that form a group, not
163 groups (see, for example, the use of the word “element” in group theory in mathematics). Thus, each
164 species belonging to the same group should be considered as an element of that group, but the group
165 itself should not be considered an element. For example, the expression “Palaeartic element” would be
166 appropriate to indicate a species belonging to the group constituted by the Palaeartic species, i.e., those
167 distributed in the Palaeartic region. Therefore, it would be correct to say that, among the birds inhabiting
168 the Italian territory, the common swift (*Apus apus*) is a Palaeartic element, and it would be equally
169 correct to say that the Palaeartic elements (in the plural) are about 4% of the Italian bird fauna, but it
170 would be not correct to say that the Palaeartic element (in the singular) represents about 4% of the
171 Italian bird fauna (chorological classification and faunal data according to Boano and Bricchetti 1989;
172 Boano *et al.* 1990; Bricchetti and Gariboldi 1997).

173 The semantically inappropriate use of “element” to refer to a group of species in biogeography originates
174 from the idea that a fauna or flora is a biogeographically heterogeneous collective, composed of various
175 groups of species that share similar distributions and possibly a common history: each of these groups is
176 an element that composes the flora or fauna. In a way, floristic and faunistic elements are regarded as the
177 biogeographic objects that constitute a certain flora or fauna.

178 However, the word “element” is polysemous and very controversial. Although the introduction of this
179 word in biogeography is usually credited to Christ (1867; see Passalacqua 2015), it was in fact first (or at

180 least simultaneously) used by Areschoug (1867; see Fattorini 2015 for a discussion). To reconstruct the
181 history of the Scandinavian flora, Areschoug identified three groups of species, which he called
182 “elements,” on the basis of both their current distribution and supposed origin. Thus his approach seems
183 to be truly related to that of “floral elements” *sensu* Passalacqua (2015). In fact, the word “element” has
184 been, and still is, used by many phytogeographers in the same way as proposed by Areschoug (1867). For
185 example, biogeographers dealing with the Australian flora have traditionally identified Australian,
186 European, Andean, Mayalan-Melannesian and Oriental elements and continue to use these terms to
187 describe the composition of Australian and New Zealand biotas (see, for example, Hooker 1859; on the
188 history of Australian biogeography, see Ebach 2012). By contrast, the use of the term “element” by
189 Christ (1867) seems much more related to the concept of “chorotype”, i.e., groups of species with similar
190 distributional patterns without any assumption about their origin (see Fattorini 2015).

191 It should also be remembered that Hooker and Thomson (1855) already used the word “element” to
192 indicate species groups based on biogeographic principles, although the criteria that these authors used
193 were not clearly explained and are hence difficult to reconstruct. Hooker and Thomson (1855) used the
194 word “element” to identify sets of taxa shared between an area under study (in their case, India) and other
195 areas with the aim of recognizing “geographical alliances or affinities”. With the emergence of the
196 dispersalist paradigm, this approach resulted in the use of the word “element” to refer to the origin of the
197 concerned taxa in a particular area (see, for example, Diels 1906; Gardner 1959; Keast 1959; Paramanov
198 1959 for the Australian flora and fauna). With this approach, elements are named to reflect their main
199 distribution, which may be outside the area under study. According to this use, the concept of element
200 may seem similar to that of distributional patterns and cenocron (and hence horofauna). However, the
201 concept of cenocron indicates a historically coherent group of species whose current distributions (i.e.
202 their distributional patterns) are a reflection of a common biogeographic history; thus each area has its
203 cenocron. By contrast, a group of species that form a certain element can have entered a given area at
204 different times and may have undergone different biogeographic histories. They thus do not necessarily
205 belong to the same cenocron.

206 To further complicate things, Engler (1882) attached to the term “element” an ecological connotation by
207 speaking of “ruderal elements,” a term referring to species that live in cities. Moreover, Engler used the
208 term element not only in a merely descriptive, phenomenological meaning, but also to indicate categories
209 based on the causes assumed to have determined present distributions, thus introducing a causal
210 (evolutionary) interpretation, which makes his use of the word “element” similar to that of Areschoug
211 and Passalacqua. In fact, this approach has its roots in Forbes (1846), who proposed a biogeographic
212 classification of the British flora into five groups of species on the basis of their assumed immigration
213 time into the British Isles, thus establishing a link between distributional patterns and biogeographic
214 history (however, note that Forbes did not use the word “element”, but “type”).

215 In summary, since Engler, the term element was used by biogeographers to indicate: (i) groups of species
216 with similar overall distribution patterns; (ii) groups of species with a similar distribution within the area
217 under study (but which may have very different overall ranges); (iii) groups of species inhabiting a
218 certain region (but which may have very different overall ranges); (iv) groups of species that require
219 particular ecological conditions (irrespective of their geographical distribution); (v) groups of species
220 supposed to have experienced the same historical events (species grouped according to the time when

221 they became a part of a given flora or fauna); (vi) species that shared similar immigration pathways (i.e.,
222 species grouped according to routes by which they migrated to a given region); (vii) groups of species
223 supposed to have originated in the same area, or which are phylogenetically related, without regards to
224 their current distribution (see Table 1 for examples).

225 This conflation of concepts was apparent already at the beginning of the twentieth century and Reichert
226 (1921) proposed to use the term “component” to refer to species with similar distributions, reserving the
227 term “element” to indicate groups of species with a common phylogenetic and/or biogeographic history.
228 After Reichert, the term “element” was used by botanists also in a broader sense, including vegetational
229 and phytosociological aspects (see Arrigoni 1974 for references). To clarify the specific meaning of the
230 word “element,” various authors attached adjectives. For example, Jerosh (1903) suggested to distinguish
231 floristic groups only based on similar geographic distribution (“geographical elements”) from groups of
232 species which shared a common history (“genetic elements”) and Wulff (1943) distinguished among
233 “geographical elements,” “genetic elements,” “migration elements,” “historical elements,” and
234 “ecological elements.” This proliferation of groupings with very different, but interrelated meanings in
235 biogeography parallels that of infra- and superspecific taxonomic categories, such as natio, ecotype,
236 ecospecies, biotype, syngameon, convivium, gamodeme, commiscuum, linneon, coenospecies,
237 superspecies, synagmeon, etc., which, roughly at the same time, characterized systematics (see, for
238 example, Arrigoni 1988 for a review).

239 Like botanists, zoogeographers used the term “element”, or “component” (generally as synonyms),
240 without clear distinction. The situation in zoogeography was further complicated by the fact that
241 zoologists classified animal species into biogeographic groups using geographical regionalization based
242 on plant distributions.

243 Under the assumption that “plant and animal distribution show a close agreement since both are
244 influenced by – and a result of – the same environmental factors” (Bodenheimer 1935), types of animal
245 distribution were forced into biogeographic units based on plant distributions. Classical examples of this
246 approach can be found in Walter (1954) and Freitag (1962), where “geographical elements” and
247 biogeographic regions largely overlap, so that species are classified into groups that reflect a plant-based
248 biogeographic division of a certain territory. With this approach, species distributions are used to divide
249 the geographical space into regions and species that coexist in a certain region are automatically assumed
250 to have a similar distribution. As a result, the same term may indicate both a type of distribution for an
251 animal and the biogeographic unit where that animal lives. For example, Freitag (1962) divided the
252 European territory into 11 regions based on species showing similar distributions (geoelements). One of
253 these regions is the Mediterranean one, and – on this basis – all species occurring only there should be
254 considered “Mediterranean elements”. But when a species is present in more than one region, it becomes
255 arbitrary to classify it with one of these regions. For example, if a species is present in both the
256 Mediterranean and the Atlantic region, is it a Mediterranean element also occurring in the Atlantic region,
257 or an Atlantic species also occurring in the Mediterranean? This situation is further complicated by the
258 fact that biogeographic units are generally recognized also on the basis of certain ecological settings, and
259 hence the same term acquires an additional ecological significance.

260 An emblematic example of the ambiguities associated with the geographical adjectives used to
261 characterize species distributions is offered by the use of the word “Saharo-Sindian” by zoogeographers.

262 The term “Saharo-Sindian” may mean that a species is distributed from the Sahara to the Sind, that a
263 species is found in a biogeographic region known as the Saharo-Sindian, or that it is simply a desert
264 species, thus becoming synonymous with “eremian” (which is also used to indicate a division of the
265 Palaearctic region including northern Africa, northern Arabia, and desert regions of Asia). Thus, the term
266 “Saharo-Sindian” was first used by Eig (1931) to determine a phytogeographical region. Then,
267 Bodenheimer (1935) used this term to refer to both a biogeographic unit (the “Saharo-Sindian” region,
268 defined by some climatic and vegetational characteristics) and a distribution type (and hence the species
269 that inhabit the Saharo-Sindian region). To distinguish between a merely geographical type of
270 distribution and an ecological characterization, Koch (1940) proposed to use the term “Saharo-Sindian”
271 to refer to a distribution type and “eremian” for an ecological characterization, while he regarded the
272 “Saharo-Sindian” province as a composite area with transitional characters. However, at the same time,
273 Gridelli (1930, 1953) used the term “eremian” to indicate both a type of distribution and a biogeographic
274 province, corresponding to the Saharo-Sindian one, without regard to species ecology.
275 This eco-geographic use of the word element can still be frequently found in modern accounts, where
276 expressions such as “tropical” and “mesic” elements refer to taxa found in a certain area but thought to
277 originate in another area with a different biome (see, for example, Ehrendorfer 1986, pp. 16, 22, 73, 82,
278 113, 227, 268, 280).

279

280

281 **The historical perspective**

282

283 Most authors assume that present distributions strongly reflect historical patterns and have used
284 geographical terms to refer to past geographical conditions. For example, Gridelli (1950) used various
285 terms to indicate different types of trans-Adriatic distributions supposed to have originated under
286 different palaeogeographical conditions (namely, via land-bridge connections between areas that are now
287 divided by the Adriatic sea). Likewise, Koch (1948) recognized a number of distribution types in the East
288 Mediterranean that he supposed to reflect past inter-island land-bridge connections. A famous example of
289 chorological groups based on both current geographical distributions and assumed biogeographic
290 histories of species, is the application of the concept of “faunal types” by Voous (1960) for European
291 birds. To further complicate things, Voous' chorological groups were also intended to individuate species
292 that are characteristic of particular biogeographic areas.

293 As a consequence of the virtually universal acceptance of the dispersalist paradigm until the mid-
294 twentieth century, some authors proposed that taxa that have similar distributional patterns also used the
295 same dispersal routes and/or originated in the same area. According to the “dispersal paradigm”, all
296 species have a center of origin from which they dispersed to assume their present distribution, even if
297 disjunct (see Cox and Moore 2010). This assumption has long dominated biogeographic thought. Its roots
298 can be traced back to the Biblical narrative of “The Flood” and “Noahs’ Ark”, but the center-of-origin-
299 dispersal model became the ruling theory in historical biogeography in the nineteenth century. Most
300 probably, Darwin's biogeographic observations about dispersal, coupled with his theory of evolution,
301 were among the most important reasons for the almost universal acceptance of the “dispersal paradigm”
302 (Baker 2007; Lomolino *et al.* 2010). It should also be noted that the idea that a species originates in a

303 certain place and then extends its range by colonizing even very distant territories fitted the overriding
304 British ethos of colonization of the nineteenth century. As Browne (1992: 468) notes, “the word most
305 used by early nineteenth-century students of animal and plant distribution patterns was ‘colonist.’ This
306 was the language of expansionist power.”

307 The dispersal paradigm led many biogeographers to assign a historical connotation to current
308 distributional patterns by assuming that they reflect, and can therefore be used to reconstruct, species
309 dispersal routes. For example, Walter (1954) and Freitag (1962) used the word “genoelements” to
310 indicate species that are assumed to have the same centre of origin. Freitag (1962) also used the word
311 “migroelements” to indicate the species that colonized a certain territory using the same assumed
312 dispersal route. To indicate current distributions that reflect past land configurations (i.e.,
313 paleogeographical conditions, as done by Koch 1948 and Gridelli 1950), Walter (1954) and Freitag
314 (1962) used the word “chronelement”.

315 Particularly influential in this sense was De Lattin's (1967) use of the word “element” (namely,
316 *Faunenelement*, i.e. “faunal elements”) to indicate the last dispersal centre of a taxon in the framework of
317 the “refuge” hypothesis. Refuges can be defined as areas into which populations retreat during periods of
318 unfavorable climates. According to the refugial center hypothesis, a number of present distributions in
319 Europe are largely dependent on effects of Pleistocene glaciations. In particular, as the glaciations
320 moulded entire biotas, an analysis of the distribution patterns of various species should lead to the
321 recognition of last-glacial refugial centers, an approach championed by De Lattin's use of “faunal
322 elements.” Echoes of De Lattin's categorization of “faunal elements” can also be found in very recent
323 literature (e.g., Schmitt 2007).

324 The “dispersal paradigm” was very pervasive in biogeography until the mid-twentieth century, when it
325 was questioned due to the rise of panbiogeography and vicariance biogeography. According to
326 panbiogeographers and vicariance biogeographers, the distributions of taxonomic groups are mainly
327 determined by range splitting of previously widespread taxa (a process named “vicariance”). The
328 question is if species achieve widespread distributions only in the absence of barriers, resulting in
329 disjunct distributions when this continuous range is divided by vicariance events, or if they are able to
330 cross barriers by jump dispersal, resulting in disjunct distributions without vicariance. Dispersalists allow
331 that dispersal (in the sense described above) takes place in many cases, whereas panbiogeographers and
332 vicariantists allow that some dispersal across barriers does occur, but feel that it is a relatively rare
333 biogeographic process. The dispersalists vs vicariantists debate that animated the biogeographic
334 community in the 70s and 80s rests on oversimplifications, because both phenomena occur in the real
335 world, and many current studies of historical biogeography attempt to disentangle the role of dispersal
336 and vicariance in determining current distribution patterns. However, the rise of vicariance biogeography
337 certainly contributed to remove the dispersalist point of view typically associated with the concept of
338 “element” and may have promoted the widespread use of the concept of “chorotype”, which does not
339 imply any historical assumption.

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341

342 **What is a chorotype?**

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344 To indicate groups of species merely based on their similar geographical distribution (i.e., without any
345 assumption about their biogeographic history), the word “chorotype” is now frequently used. The
346 creation of this word has been credited to La Greca (see Morrone 2014), who proposed a general
347 classification of the distribution patterns of the Italian fauna (La Greca 1964). In fact, La Greca never
348 explicitly used the word “chorotype,” but rather always used the expression “chorological categories”
349 (see Fattorini, 2015). It was his followers, especially Vigna Taglianti *et al.* (1993, 1999), who established
350 the equivalence “chorological category” = “chorotype”, although La Greca himself (1975) specified that
351 the expression “chorological category” was to be considered equivalent to the German *Verbreitungstyp* or
352 the French *aréotype*, which are in turn equivalent to the word “chorotype” as used by La Greca’s
353 followers.

354 La Greca defined his “chorological categories” as “standard ranges of statistic[al] value, deriving of [sic!]
355 many species with nearly similar geographical distribution” (La Greca 1975: 127). Thus, La Greca used
356 the expression “chorological categories” to indicate recurrent types of species ranges and this expression
357 is maintained here for the sake of simplicity, although it is different from the meaning of “chorological
358 categories” as used by Passalacqua (2015, p. 611: “criteria on which biogeographical units are based”).

359 Moving from the observation that different species tend to present similar ranges, La Greca identified
360 some (theoretical) groups (his “categories”) into which (concrete) species ranges can be grouped through
361 an inductive and recursive process. In this process, species ranges are mapped, their contours are
362 compared, and species with nearly coincident ranges are classified with the same group, i.e., they form a
363 chorotype. After a chorotype is defined by multiple overlapping species ranges, any other species with a
364 similar range is attributed to that chorotype. La Greca clearly explained this procedure in a paper
365 published in 1963 in a journal with small circulation. Thus, to expand its diffusion, it was reprinted –
366 without modifications – in 1964 in a more widespread journal (La Greca 1964).

367 La Greca’s approach is merely phenomenological, in the sense that it is aimed at identifying recurrent
368 types of species distributions without any assumption about the causes of the patterns.⁶

369 Although La Greca has been frequently credited as the “father” of chorotypes (see Morrone 2014), the
370 use of chorological groups, conceptually identical to that brought forward by La Greca, has a much
371 longer history in zoogeography. The first botanical work that can be properly considered a true
372 application of the concept of chorotype *sensu* La Greca is probably the aforementioned study on the
373 Alpine flora by Christ (1867), where species are classified into a few groups on the basis of their overall
374 distribution and supposed centre of origin. Hofmann (1873), in his analysis of the distribution of the
375 European butterflies, grouped them into seven chorological groups (*geographische Gruppen*) which
376 conceptually correspond to chorotypes as defined by La Greca. After Hofmann’s pioneering work, several
377 zoologists used chorological groups that are conceptually identical to those proposed by La Greca. One

⁶ In fact, La Greca attached a possible (but not necessary) historical interpretation to his chorological categories by assuming that species belonging to the same chorological category also probably shared a similar biogeographical history. In fact, ontological parsimony suggests that if several species have similar distributions, this should be explained by a common cause, rather than independent processes. This point of view is more or less explicit in La Greca’s paper, but his followers preferred to avoid attaching a casual explanation to chorotypes. This implication was definitively removed by Vigna Taglianti *et al.* (1994), who used chorotypes as merely descriptive tools.

378 of the most remarkable examples is an influential paper by Holdhaus (1929), where a number of
379 chorological groups are presented for the Palaearctic insects. Most of these groups correspond to (and
380 also have the same names as) La Greca's "categories". Similarly, chorological groups largely
381 corresponding to those presented by La Greca were identified and used in a series of papers by Gridelli
382 (1930, 1933, 1939, for examples). Finally, Hooker and Thomson (1855) already classified species into
383 biogeographic groups in such a way that they also seem to resemble chorotypes. However, Hooker and
384 Thomson did not refer to merely recurrent patterns of distribution based on overlapping species ranges,
385 but, as was mentioned already, to sets of taxa shared between the area under study (India) and other areas
386 with the aim of recognizing "geographical alliances or affinities". Thus, although Passalacqua (2015)
387 considered Hooker and Thomson's categories as an example of chorotypes, this work may be more
388 properly viewed as a precursor of the biogeographic analyses based on the identification of similarities
389 among biotas (Lomolino *et al.* 2010), not of chorotypes.

390 The "chorological categories" proposed by La Greca for the Italian fauna had been largely adopted by
391 Italian zoogeographers up until 1993, when Vigna Taglianti *et al.* proposed a new classification and
392 nomenclature of chorotypes for the W-Palaearctic fauna, which was further revised in 1997 (Vigna
393 Taglianti *et al.* 1997) and rapidly replaced that of La Greca (more than 254 citations retrieved by Google
394 Scholar on 24th February 2016).

395 Although these two papers mostly contributed to the dissemination of the use of the word chorotype,
396 Vigna Taglianti *et al.* did not coin this word. The word chorotype was apparently introduced by Frizzell
397 (1933, p. 646), who used it in taxonomy to indicate "A fossil specimen collected from the same stratum
398 as the type, but from a neighboring locality" (see Fattorini 2015). In biogeography, it was introduced by
399 Baroni Urbani *et al.* (1978) to indicate groups of species with a similar distribution within an area, thus
400 with a different meaning from that of the "chorological categories" (or equivalent expressions) based on
401 overall ranges⁷. A few years prior to Baroni Urbani *et al.*'s paper, Pignatti and Sauli (1976) conducted a
402 study on the Italian angiosperms, where each species was assigned to a chorotype on the basis of their
403 overall distribution. This was thus in a sense analogous to the approach taken by La Greca. However,
404 Pignatti and Sauli used the expression "chorological type", not the word "chorotype" (although the
405 meaning was obviously the same). Likewise, "chorological type", not "chorotype", was used by Pignatti
406 (1982), although the meaning is analogous.

407 In summary, there are now two different uses of chorotypes. A first use, promoted by La Greca (1963,
408 1964) and Vigna Taglianti *et al.* (1993, 1999) in zoology and by Pignatti and Sauli (1976) and Pignatti
409 (1982) in botany, refers to groups into which species with roughly similar overall ranges can be
410 classified. This corresponds to the definition given by Morrone (2014: "items of a classification based on
411 [...] the comparative analysis of the geographical ranges of species"), and is referred to as "global

⁷ Baroni Urbani *et al.* (1978, p. 42) used the expression "numerical chorotypes" to indicate small groups of species forming "elementary distributional patterns." Then, they grouped chorotypes into larger groups ("basic types of distribution"). The two categories are identified as two different cut-off levels of the same dendrogram that grouped species according to their distribution. Because they are conceptually identical, Fattorini (2015) did not distinguish between them, and used the expression "regional chorotypes" also for Baroni Urbani *et al.*'s major groups.

412 chorotype” by Fattorini (2015). This concept of chorotype is also identical to that of “geoelement”,
413 “geographical element”, “arealtype” or *Verbreitungstyp* (see Wulff 1943; Schilder 1956; Seddon 1971).
414 A different use, which corresponds to that indicated by Baroni Urbani *et al.* (1978), refers to groups of
415 species with statistically similar distributions *within* a certain region (*not* on the basis of their *overall*
416 ranges), and is referred to as “regional chorotype” by Fattorini (2015). This second concept of chorotype
417 dates back to Watson's (1832, 1835, 1847) classification of the British flora into seven groups according
418 to species' distribution within the British Isles, which displays a logic perfectly identical to that of Urbani
419 *et al.* (see Fattorini 2015).

420 Global chorotypes correspond to the chorotypes as defined by Vigna Taglianti *et al.* (1993, 1999), to the
421 chorological types *sensu* Pignatti and Sauli (1976), to the chorotypes *sensu* Pignatti (1982), to the
422 “chorological categories” *sensu* La Greca (1963, 1964) and to similar expressions used by previous
423 authors, such as Hoffmann, Holdhaus or Gridelli. These are “abstractions” used to summarize recurrent
424 species ranges, being therefore roughly similar to the “generalized tracks” of Croizat (1958). They are
425 generally used both as a practical tool to shortly express the distribution of species and as an analytical
426 tool to draw some inference about the origin of faunas or floras.

427 Regional chorotypes (as used by Baroni Urbani *et al.* 1978; Marquez *et al.*, 1997; Vergas *et al.* 1997;
428 Sans-Fuentes and Ventura 2000; Olivero *et al.* 2001; Ferrer-Castan and Vetaas 2003; Gómez-González *et*
429 *al.* 2004; Báez *et al.* 2005; Real *et al.* 2008) refer to groups of species that roughly occupy the same
430 geographical units (such as regions or grid cells) within a certain area, without reference to their overall
431 distribution, and operationally also correspond to the concept of Hausdorf and Hennig's (2003) “biotic
432 element”.

433 The concept of chorotype should be distinguished from other, allied terms. It must be stressed that a
434 chorotype is an abstraction used to group species that have similar distributions but can belong to
435 completely different taxonomic groups, occupy very different biotopes, have unrelated biogeographic
436 histories, etc. Thus, chorotypes are different from faunas and floras, which include all the species that live
437 in a certain region and which belong to different chorotypes. Chorotypes may be assimilated into
438 Morrone's (2014) general concept of biota, under which the concepts of areas of endemism and
439 generalized tracks should be also grouped. However, areas of endemism are a result of regionalization,
440 whereas chorotypes identify species groupings, not areas (and, as a matter of fact, a certain area may
441 contain species with completely different chorotypes). Differences between chorotypes and generalized
442 tracks are subtler. Chorotypes are obtained by superimposing species distributions; after chorotypes have
443 been defined on the basis of a set of species, any other species that shows a distribution similar to that of
444 a certain chorotype is classified as belonging to that chorotype. A track is a line drawn on a map that
445 connects the different localities or distribution areas of a particular taxon or group of taxa (Craw *et al.*
446 1999, p. 20) and is therefore a representation of the geographical range of a taxon in which space
447 geometry is interpreted as an explicit component (see Morrone 2009). A set of two or more individual
448 tracks, which are compatible or congruent according to a specified criterion (for example, shared
449 baselines or compatible track geometries), forms a generalized track (Crisci *et al.* 2003, p. 57).
450 Generalized tracks are assumed to be the result of a common Earth-taxon history, i.e. they are assumed to
451 reflect a common response of different taxa to the same historical events (Croizat 1958). In contrast, no

452 underlying mechanism is assumed to produce the species distributions that are assigned to the same
453 chorotype.

454 Recently, Hausdorf (2002) defined the concept of “biotic elements” as groups of taxa whose ranges are
455 significantly more similar to each other than those of taxa of other such groups (see also Hausdorf and
456 Hennig 2007). Like the other terms discussed so far, this term as well has a complicated history. It was
457 introduced by Dunn (1931) to refer to a subset of taxa within a fauna. Müller (1973, p. 3) defined a biotic
458 element as the “species and subspecies which resemble each other in their geographical distribution, and
459 which can be ascribed to a single dispersal centre”, thus introducing a historical (dispersalist)
460 interpretation. Reig (1981, p. 27) defined a biotic element as a group of taxa that form a recognizable unit
461 because of their common biogeographic origin, membership to a given cenocron, or autochthonous or
462 allochthonous character. More in general, Morrone’s (2014) review shows that “biotic element” has been
463 also used to identify both (1) a subset of taxa within a fauna, and (2) species and subspecies which
464 resemble each other in their geographical distribution, and which can be ascribed to a single dispersal
465 centre. These definitions may correspond, in certain circumstances, to that of global chorotype. The
466 concept of biotic element *sensu* Hausdorf, in contrast, can be assimilated into that of regional chorotype.
467 However, whereas identification of regional chorotypes does not make any assumption about the
468 processes that led to the origin of similar ranges, biotic elements are assumed to emerge as a result of
469 vicariance events (Hausdorf and Hennig 2007).⁸ Also, biotic elements *sensu* Hausdorf should belong to
470 the same area of endemism (“the ranges of the species that have originated in the same area of endemism
471 will be more similar to each other than ranges of species that have originated in other areas of
472 endemism”, Hausdorf and Hennig 2007, p. 717), whereas this is not implied in the concept of chorotype.

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474

475 **More things with the same name, more names for the same thing**

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477 As a result of the lack of consistence among authors in the use of concepts, also the terminology used to
478 name chorological groups is extremely confused. For example, to identify the species with a distribution
479 restricted to the Mediterranean Basin, certain authors use the word “Holo-Mediterranean”, but others
480 simply “Mediterranean”, and the same term “Mediterranean” is also frequently used in an ecological
481 sense, to indicate species that live in areas with “Mediterranean” climate and vegetation, without regard
482 to their geographical location. Hence, though the meaning of the most common terms used to identify
483 recurrent geographical distributions (e.g., amphipacific, amphiatlantic, panboreal, circumpolar antarctic,
484 arctic-alpine, etc.) seems to be clear to every biologist (Udvardy 1969; Seddon, 1971), it is actually
485 difficult to know with certainty what they really mean, because these terms are often used casually,
486 without clear definitions.

487 To avoid confusion, various biogeographers have proposed explicit definitions of the distribution types
488 they use (either in the sense of element or chorotype). For example, within the European areas, St. Claire
489 Deville (1930) divided the Coleoptera of the British Isles according to their European distributions into a
490 number of clearly defined (but not named), strictly geographical groups and subdivisions, while a number

⁸ However, Hausdorf (2002, p. 651) specified that “biotic elements” are not necessarily generated by vicariance events, but can also originate via dispersal and speciation.

491 of types of distribution were clearly defined and termed by Holdhaus (1929) and Gridelli (1930, 1933,
492 1939) for the Mediterranean areas. After Holdhaus' and Gridelli's papers, more general classifications
493 with accurate and explicitly defined terminology were proposed by Meusel (1943), Hulten (1950),
494 Matthews (1954), Meusel *et al.* (1965) and Seddon (1971) for the European flora and fauna. Likewise, a
495 scheme for the North American flora was proposed by Dice (1943).

496 The importance of the adoption of an explicit scheme of classification dramatically appears in studies
497 where some consistence is necessary to allow comparisons. For example, a unified scheme of types of
498 distribution was depicted by Czechowski and Mikolajczyk (1981) and followed by all authors working on
499 different animal groups in the framework of a general project on the urban fauna of Warszawa.

500 More generally, unequivocal schemes of classification for distribution types are desirable in any floristic
501 or faunistic research, because only analyses using the same scheme can be compared. Thus, when La
502 Greca (1963, 1964) proposed the aforementioned general classification of the distribution patterns of the
503 Italian fauna, with clearly defined ranges, almost all the Italian zoogeographers accepted this scheme.
504 However, most authors modified the original categories proposed by La Greca to obtain new categories
505 fitting more accurately the distribution patterns of the animal groups they were studying, which led to a
506 proliferation of new categories and originated a new climate of confusion. To have a new and broader
507 standard, Vigna Taglianti *et al.* (1993, 1999) proposed the aforementioned revised classification and
508 nomenclature of the main geographical patterns of the West Palaearctic fauna, which is now the one most
509 frequently used.

510

511

512 **Conclusions**

513

514 Four terms are now used, sometimes as synonyms, to express groups of species with similar distributional
515 patterns: chorological category, element, chorotype and component. These terms have a long and
516 complicated history since they were used in the context of very different research programmes and since
517 terminological consistency was not always preserved. On the basis of history outlined in this paper, I
518 would make some recommendations for a correct and unambiguous use.

519 The word "category" should not be used to indicate species groups, but – as suggested by Passalacqua
520 (2015, p. 611) – to indicate "the criteria on which the units should be based". In this sense, elements,
521 chorotypes and components are three types of "categories."

522 The term "component" is currently used in ecology to denote the biotic or abiotic constituent of an
523 ecosystem (Passalacqua 2015). Its use in biogeography (typically as a synonym for element) should be
524 avoided.

525 The terms "element" and "chorotype" should be used to express different concepts. The word "element"
526 has been used to identify both a group of species defined according to the biogeographic areas they
527 occupy and a group of species with similar biogeographic history. Because of the long tradition of this
528 twofold meaning, the term is ambiguous. So, its use should be always associated with an explicit
529 definition to avoid further confusion.

530 Finally, the word chorotype should be used to define groups of species with similar ranges when no
531 causal assumption is made. The expression "global chorotypes" should be used in reference to groups of

532 species with similar overall ranges. The expression “regional chorotypes” should be used for groups of
533 species that roughly occupy the same geographical units within a certain area, without reference to their
534 overall distributions.

535 My reconstruction of the history of the words used by biogeographers to indicate species groupings
536 illustrates how conceptually complex a seemingly straightforward relationship - that between organisms
537 and the places they inhabit - can get. This complexity cannot be resolved by reducing it to one concept,
538 but only through building a clear architecture of complementary concepts. In particular, the two concepts
539 of element and chorotype reflect two different research programmes: one (chorotype) devoted to group
540 species with similar ranges into general distributional patterns for descriptive purposes, the other
541 (element) to group species according to their hypothesized history and biogeographic affinities in order to
542 reconstruct biogeographic processes. These two research programmes are not mutually exclusive but
543 rather complementary, and failure to distinguish between them has created confusion in the use of
544 biogeographic terminology. Biogeographic concepts are extremely varied and subtle, even if they may
545 seem very simple at first sight, so that one always needs to analyse them carefully from historical and
546 philosophical perspectives to avoid confusion and misunderstanding.

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Definition/Use	Nomenclature	Authors
Groups of species with similar distributions (without any assumption about their origin)	Chorological categories	La Greca (1963, 1964, 1975)
	Chorotypes	Vigna Taglianti <i>et al.</i> (1992, 1999)
	Geographical groups (<i>geographische Gruppen</i>)	Hofmann (1873)
	Elements	Christ (1867), Birks, (1987), McLaughlin, (1994), Hausdorf, (2002), Finnie <i>et al.</i> (2007)
	Geographical elements	Jerosh (1903), Wulff (1943)
	Arealtypes (<i>Arealtypen/arealtypen Gruppen</i>)	Wangerin (1932), Meusel & Jäger (1992)
	Chorological type	Ojeda <i>et al.</i> (1995), Ferrer-Castan and Vetaas (2003)
Groups of species with similar distributions within a particular (bio)geographical region	Elements	Christ (1867)
Groups of species inhabiting a particular (bio)geographical region	Elements	Engler (1882), Braun-Blanquet, (1919), Bharucha and Meher-Homji (1965), Arrigoni (1974)
	Geographical elements	Wulff (1943)
	Geoelements / fundmaental distributions (<i>Hauptverbreitung</i>)	Walter (1954), Freitag (1962)
Groups of species with similar ecology	Elements	Engler (1882)
	Ecological elements	Wulff (1943)
Groups of species shared between a given area and other areas	Geographical alliances or affinities	Hooker and Thomson (1855)
Groups of species with statistically similar distribution within a certain region	Chorotypes	Baroni Urbani <i>et al.</i> (1978)
Groups of species that are assumed to reflect a common history/immigration routes	Elements	Engler (1882), Wulff (1943), Voous (1960)
Groups of species that have a similar distribution	Component	Reichert (1921)
Groups of species that originated in the same area	Genetic elements	Jerosh (1903), Reichert (1921), Wulff (1943)
	Genoelements (species with the same centre of origin)	Walter (1954), Freitag (1962)
	Element	De Lattin (1967)
Groups of species that are assumed to	Chronoelements (species which	Walter (1954), Freitag

had a common history	occupied the same area in the past)	(1962)
Groups of species that became a part of a given flora/fauna in the same period	Historical elements	Wulff (1943)
Groups of species that immigrated in a certain area using the same dispersal routes	Migroelements	Freitag (1962)
	Migration elements	Wulff (1943)

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