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Strapline: Correspondence
Running header: Correspondence

On the concept of chorotype

ABSTRACT

Recent reviews of the meaning of the word 'chorotype' in biogeography have led to contrasting definitions and a confusion of concepts. This is because 'chorotype' has been used by different authors to express two different concepts: (1) groups of species with overlapping ranges (overall distributions), and (2) groups of species with a similar distribution within a certain area. To avoid confusion, I suggest the term 'global chorotype' be used to indicate a group into which species with similar ranges can be classified; and 'regional chorotype' be used for a group of species with similar distributions within a certain region. Although the global chorotype represents the worldwide spatial responses of species to historical and environmental pressures, and does not vary with the area under consideration, a particular species might be classified into different regional chorotypes in different study areas.

Keywords

areography, biotic element, chorological categories, global chorotype, regional chorotype, species distribution, species range

The concept of the chorotype has been reviewed recently by Morrone (2014) and Passalacqua (2015). According to Morrone:

> [T]his term was introduced by La Greca (1963, 1964, 1975). Chorotypes were defined as 'items of a classification based on distribution patterns such as deduced from the comparative analysis of the geographical ranges of species, genera and higher taxa'

[…] or 'groupings of species with similar distribution patterns' […].

(Morrone, 2014, p. 388)

By contrast, according to Passalacqua:

> Baroni-Urbani *et al.* (1978) coined the term 'chorotype' […], aiming to identify distribution categories and to group organisms with '[…] similar geographical distribution into 'types' of distribution'.
>
> (Passalacqua, 2015, p. 612)

These two definitions may seem similar, but refer to different concepts, as also shown by the contradiction in the attribution of the authorship of the word: the definition given by Morrone and attributed to La Greca refers to the identification of recurrent patterns of distribution on the basis of the overall ranges of the species, whereas that given by Passalacqua and attributed to Baroni Urbani and colleagues is based on the distribution shown by different species within a certain area, not on their overall ranges.

To clarify the concept(s) of chorotype it is first important to reconstruct how it was introduced into the field of biogeography. Not only did La Greca and Baroni Urbani and colleagues use the concept of 'chorotype' with very different meanings, but neither La Greca nor Baroni Urbani and colleagues actually coined this word. La Greca never explicitly used the word 'chorotype', but rather always used the expression 'chorological categories'. It was his followers, namely Vigna Taglianti *et al.* (1993, 1999), who established the equivalence of 'chorological category' and 'chorotype' (see below). La Greca defined his chorological categories as 'standard ranges of statistic[al] value, deriving of[*sic*] many species with nearly similar geographical distribution' (La Greca, 1975, p. 127). Thus, La Greca's chorological categories indicate recurrent types of species ranges, and this expression is maintained here for the sake of simplicity, although it is different from the meaning of 'chorological categories' as used by Passalacqua ('criteria on which biogeographical units are based').

The aim of La Greca's chorological categories was to establish a standardized nomenclature for recurrent species ranges. Moving from the observation that different species tend to present similar ranges, La Greca identified some (theoretical) groups (his 'categories') into which (concrete) species ranges could be grouped through an inductive and recursive process. In this process, species ranges are mapped, their contours are compared, and species that show largely coincident ranges are classified into the same group, i.e. a chorotype. After a chorotype is defined by multiple overlapping species ranges, any other species with a similar range is attributed to that chorotype (see Fig. 1a). La Greca clearly explained this procedure with reference to the Italian fauna, in a paper initially published in 1963 (La Greca, 1963). This paper first appeared in a journal of limited circulation, and so, to increase its diffusion, it was reprinted unaltered in 1964 in a more widely read journal (La Greca, 1964). For simplicity's sake, I will refer here only to this second, more accessible version.

La Greca's (1964) paper was immensely successful, because it provided zoogeographers interested in the Mediterranean faunas with a practical tool for assigning species ranges to pre-established and unambiguously defined chorological groups. As observed by Udvardy, who was probably unaware of La Greca's paper:

> When the zoogeographer scrutinizes and compares distribution areas on the map and globe, he often uses a special terminology for certain commonly occurring area types [chorotypes]. […] Though the meaning of these terms […] is by and large clear to every biologist and geographer, it is difficult to define them accurately because they are used so often and without definition in the literature.
>
> (Udvardy, 1969, p. 217)

La Greca's work was popular, especially among entomologists, precisely because it addressed this lack of a standard nomenclature to identify recurrent distributional ranges. Because of the popularity of this 1964 paper, La Greca he has been frequently credited as the 'father' of chorotypes, but the use of chorological groups conceptually identical to those proposed by La Greca has a much longer history in zoogeography, albeit one that is frequently overlooked. To my knowledge, the first author to explicitly notice that different animal species may have similar ranges, and that these ranges can be classified into a limited number of groups, was Hofmann (1873). In his PhD thesis, he analysed the distribution of the European butterflies by classifying them into seven chorological groups ('geographische Gruppen'; see Appendix S1 in Supporting Information). Although Hofmann was the first to define and use chorotypes as discussed here, at least in zoogeography, the idea of grouping species according to their ranges has its roots in some earlier phytogeographical papers. For example, Hooker & Thomson (1855) classified species into biogeographical groups, although they did not refer to merely recurrent patterns of distribution based on overlapping species ranges, but rather to sets of taxa shared between the area under study (India) and other areas (Appendix S1) with the aim of recognizing 'geographical alliances or affinities'. Thus, although Passalacqua (2015) listed Hooker & Thomson's work among those that used the concept of chorotype, it should be probably better considered a precursor of the biogeographical analyses based on the identification of biotic similarities among regions, rather than an example of chorotypes. Similar approaches to that of Hooker & Thomson can also be found in Forbes (1846) and Areschoug (1867). Forbes proposed a biogeographical classification of the British flora into five groups of species on the basis of their immigration time into the British Isles (Appendix S1). Similarly, to reconstruct the history of the Scandinavian flora, Areschoug identified three groups of species (which he called 'elements') on the basis of both their current distribution and supposed origin (Appendix S1). Forbes' and Areschoug's intention was to recognize species groups within a certain area according to their immigration routes, in turn based on a biogeographical regionalization of the study area. Thus, their approach seems to be more strictly related to 'floral elements' *sensu* Passalacqua (2015) than to chorotypes (which are merely geographical recurrent patterns of species ranges), although the two concepts do not appear to be clearly distinguishable in these works.

The first botanical work that can properly be considered a true application of the concept of chorotype *sensu* La Greca is probably the study of the Alpine flora by Christ (1867), in which species are classified into a few groups on the basis of their overall distribution (Appendix S1) and supposed centre of origin. Thus, although Passalacqua considers Christ's groups to be an example of the concept of 'element', they might more properly be considered as true chorotypes, as also shown by their overlaps on Christ's map. It is interesting to note that, although published in 1867, Areschoug's work was probably submitted earlier, since it appeared in the 1866 volume of a series. Thus, Christ cannot alone be credited with the introduction of the world 'element', because it was first (or at least simultaneously) used by Areschoug. Moreover, Hooker & Thomson (1855) had already used the word 'element' to indicate species groups defined on biogeographical principles. It is thus difficult to identify any clear authorship for this word.

After Hofmann's pioneering work, several zoologists used chorological groups that are conceptually identical to those proposed by La Greca. One of the most remarkable examples is an influential paper by Holdhaus (1929), in which a number of chorological groups for the Palaearctic insects were presented. Most of these groups correspond to (and share the names of) La Greca's 'categories'. Similarly, chorological groups largely corresponding to those presented by La Greca were identified and used in a series of papers by Gridelli (1930, 1933, 1939, for example). Thus, La Greca cannot be considered the first author who defined chorological groups, although the wide dissemination of his paper led most people to credit him with the origin of this concept. This belief among his followers was probably generated by the fact that – quite surprisingly – there are no references to previous works in La Greca's paper.

Not only did La Greca not use the word 'chorotype' in his 1964 (or 1963) paper, he also maintained the expression 'chorological categories' in a paper published in 1975. In this later paper, however, he specified that the expression 'chorological category' was to be considered equivalent to the German *Verbreitungstyp* or the French *aréotype*, which are in turn equivalent to the word 'chorotype' as used by La Greca's followers.

The 'chorological categories' proposed by La Greca for the Italian fauna were widely adopted by Italian zoogeographers, until Vigna Taglianti *et al.* (1993) proposed a new classification and nomenclature of chorotypes for all the Western Palaearctic fauna. Vigna Taglianti and colleagues used the word 'chorotype' exactly in the same sense as La Greca's 'chorological category'. Probably because of their wider applicability to the Western Palaearctic region, the chorotypes proposed by Vigna Taglianti *et al.* (1993) rapidly replaced those of La Greca (focused on species inhabiting Italy) and contributed to the diffusion of the word 'chorotype' in lieu of La Greca's expression 'chorological category'. After a few years, Vigna Taglianti *et al.* (1999) published a new version of their chorotypes and this updated classification and nomenclature is now in wide use (more than 239 citations retrieved by Google Scholar on 8 June 2015).

Although these two papers made the greatest contribution to the dissemination of the word 'chorotype', Vigna Taglianti *et al.* (1993, 1999) did not coin this word (and nor did Baroni Urbani *et al.*, 1978). In fact, the word 'chorotype' has a long, complicated and so far largely ignored history. This word was first introduced, to my knowledge, in taxonomy, not in biogeography. The earliest occurrence I was able to find is in a paper by Frizzell (1933, p. 646), who used 'chorotype' to indicate a 'fossil specimen collected from the same stratum as the type, but from a neighboring locality'. Thus, in this particular sense, a chorotype is one of the specimens from which a fossil taxon is described. Later, Schilder (1952, p. 19) proposed the word 'chorotype' in bionomenclature to indicate particular forms occurring in specific localities, by analogy with the use of the word 'ecotype' to indicate local forms associated with particular ecological conditions. Various recent dictionaries (Maggenti *et al.*, 2005; Lawrence, 2008; Hawksworth, 2010), probably based on Schilder, define the word 'chorotype' as 'a local type', although the use of the word chorotype with this meaning is probably very rare and I have not been able to find any occurrence. In the context of palaeobiogeography, Westermann (2000) used the word 'chorotype' in a different way, to indicate a typical region of a biochore. Finally, it is interesting to note that the word 'chorotype' is also used in social geography to indicate recurrent forms of the organization of the geographical space (see Brunet *et al.*, 1993). Thus, although Baroni Urbani *et al.* (1978) cannot be credited as the authors who coined the word 'chorotype', they were probably the first to use it in biogeography, although they used it to indicate a group of species with a similar distribution within an area, thus with a different meaning from 'chorological categories' (or equivalent expressions) based on overall ranges.

A few years earlier, Pignatti & Sauli (1976) conducted a study on the Italian angiosperms, in which each species was assigned to a chorotype on the basis of its overall distribution. This was thus in a sense analogous to the approach taken by La Greca, but Pignatti & Sauli used the expression 'chorological type', not the word 'chorotype' (although the meaning was obviously the same). Likewise, 'chorological type', not 'chorotype', was used by Pignatti (1982), although the meaning is analogous.

In summary, the use of chorotypes, as promoted by La Greca (1963, 1964) and Vigna Taglianti *et al.* (1993, 1999) in zoology – and by Pignatti & Sauli (1976) and Pignatti (1982) in botany – refers to groups into which species with similar overall ranges can be classified, corresponds to the meaning reported by Morrone (2014, p. 388) ('items of a classification based on […] the comparative analysis of the geographical ranges of species') and can be assimilated into Morrone's concept of biota. This concept of chorotype is also identical to that of 'geoelement', 'geographical element' or 'arealtype' as commonly used by most authors (see Wulff, 1943). For example, it corresponds perfectly to the definition of 'geographical element' given by Seddon:

> Distributions that are centred in the same region and whose boundaries extend in broadly the same directions can be therefore grouped together and regarded as members of the same geographical element. Of course, the size and extent of the areas of member species may vary and their boundaries often do not coincide.
>
> (Seddon, 1971, p. 31)

The word 'chorotype' is now generally used in biogeography with a different meaning, which corresponds to that indicated by Baroni Urbani *et al.* (1978), recalled by Passalacqua (2015) and which can be assimilated into Morrone's concept of cenocron. This second concept of chorotype was used by Baroni Urbani *et al.* (1978) to identify a group of species with statistically similar distributions *within a certain region* (and not on the basis of their overall ranges) (Fig. 1b) and dates back to Watson's (1832, 1835, 1847) classification of the British flora (Appendix S1). In particular, in *Cybele Britannica*, which is the final development of his earlier studies, Watson (1847) classified the British flora into seven groups according to species' distributions within the British Isles following logic identical to that of Baroni Urbani *et al.* (1978).

The difference between these two concepts of chorotypes may appear subtle and they were indeed confused in Passalacqua's paper. For example, Passalacqua (2015) explicitly refers to the concept of chorotype *sensu* Baroni Urbani *et al.* (1978), but also considers, as an example of the use of this word, Pignatti (1982). Although so far overlooked, this difference is substantial and should be made clear to avoid further confusion in biogeographical literature. Chorotypes as defined by Vigna Taglianti *et al.* (1993, 1999; hereafter simply *sensu* VT) ['chorological types' *sensu* Pignatti & Sauli (1976); 'chorotypes' *sensu* Pignatti (1982); 'chorological categories' *sensu* La Greca (1963, 1964); and similar expressions used by previous authors such as Hoffmann, Holdhaus and Gridelli] are abstractions used to summarize recurrent species ranges, being therefore similar to the generalized tracks of Croizat (1958). They are generally used both as a practical tool to concisely express the distributions of species and as an analytical tool to draw inferences about the origin of faunas or floras. These chorotypes are identified by superimposing distributional maps of species' global ranges. Species ranges with similar shapes are put in the same group, i.e. the same chorotype, which is named after the main geographical area(s) included within its boundaries (Fig. 1).

By contrast, the word 'chorotype' as used by Baroni Urbani *et al.* (1978; hereafter *sensu* BU) refers to a group of species that roughly occupy the same geographical units (e.g. regions or grid cells) within a certain area, without reference to their overall distribution. The word 'chorotype' has been used with this second meaning in a number of studies (see, for example, Marquez *et al.*, 1997; Vargas *et al.*, 1997; Sans-Fuentes & Ventura, 2000; Olivero *et al.*, 2001; Ferrer-Castán & Vetaas, 2003; Gómez-González *et al.*, 2004; Báez *et al.*, 2005; Real *et al.*, 2008) and operationally also corresponds to the concept of Hausdorf & Hennig's (2003) biotic element.

Because of this basic difference in the area treatment (overall ranges versus distribution within a study area), species with the same chorotype *sensu* VT may belong to different chorotypes *sensu* BU, even in the same study area. For example, the ground beetles *Cicindela gallica* and *Cicindela sylvicola* can both be assigned to the Central European chorotype *sensu* VT, but the former belongs to a Western Alpine chorotype *sensu* BU and the latter to an Alpine–Apenninic chorotype *sensu* BU. Equally, the same chorotype *sensu* BU may include species with very different chorotypes *sensu* VT. Indeed, as already observed by Seddon (1971) with reference to the use of total ranges versus regional distributions, two species that have a virtually identical distribution in a certain study area may have completely different overall distributions. This is clearly illustrated by the case of the ground beetles *Agonum livens* and *Licinus punctatulus*, two species with very different ranges overall but the same south-easterly distribution in England (Fig. 2). Thus, except for endemics, there is no obvious correspondence between chorotypes *sensu* VT (based on total distribution) and chorotypes *sensu* BU (based on distribution within an area). In the example illustrated in Fig. 2, both species might be classified into the same chorotype *sensu* BU (say a southern England chorotype), but *Agonum livens* would be assigned to the Central European and *Licinus punctatulus* to the Mediterranean chorotype *sensu* VT.

Moreover, the same species can be classified into various chorotypes *sensu* BU when different study areas are considered, whereas the chorotype *sensu* VT is independent of the study area. For example, the ground beetle *Carabus sylvestris*, which is distributed in Austria, the Czech Republic, Hungary, Italy, Liechtenstein, Poland, Romania, Slovakia, Slovenia, the Ukraine and the Netherlands, belongs to the Central European chorotype *sensu* VT, but its chorotype *sensu* BU will vary according to the study area: on the basis of its distribution in Italy, this species was classified in an Alpine chorotype by Baroni Urbani *et al.* (1978), but it would be probably classified in a 'Southern' chorotype in a study on the Denmark fauna.

In general, with the exception of endemics, it is obvious that for a given species, its chorotype *sensu* BU will refer to a region within the area represented by its chorotype *sensu* VT. Thus, I suggest using the expression 'global chorotypes' to identify categories used to summarize recurrent species ranges (i.e. chorotypes *sensu* VT) and 'regional chorotypes' to indicate groups of species that have a similar distribution within a certain study area (i.e. chorotypes *sensu* BU). From an operational point of view, if the entire world is considered in the application of the BU concept, then the global chorotype can be considered a special case of the BU definition.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Excerpts from works by Hofmann, Hooker & Thomson, Forbes, Areschoug, Christ and Watson.

Editor: Liliana Katinas

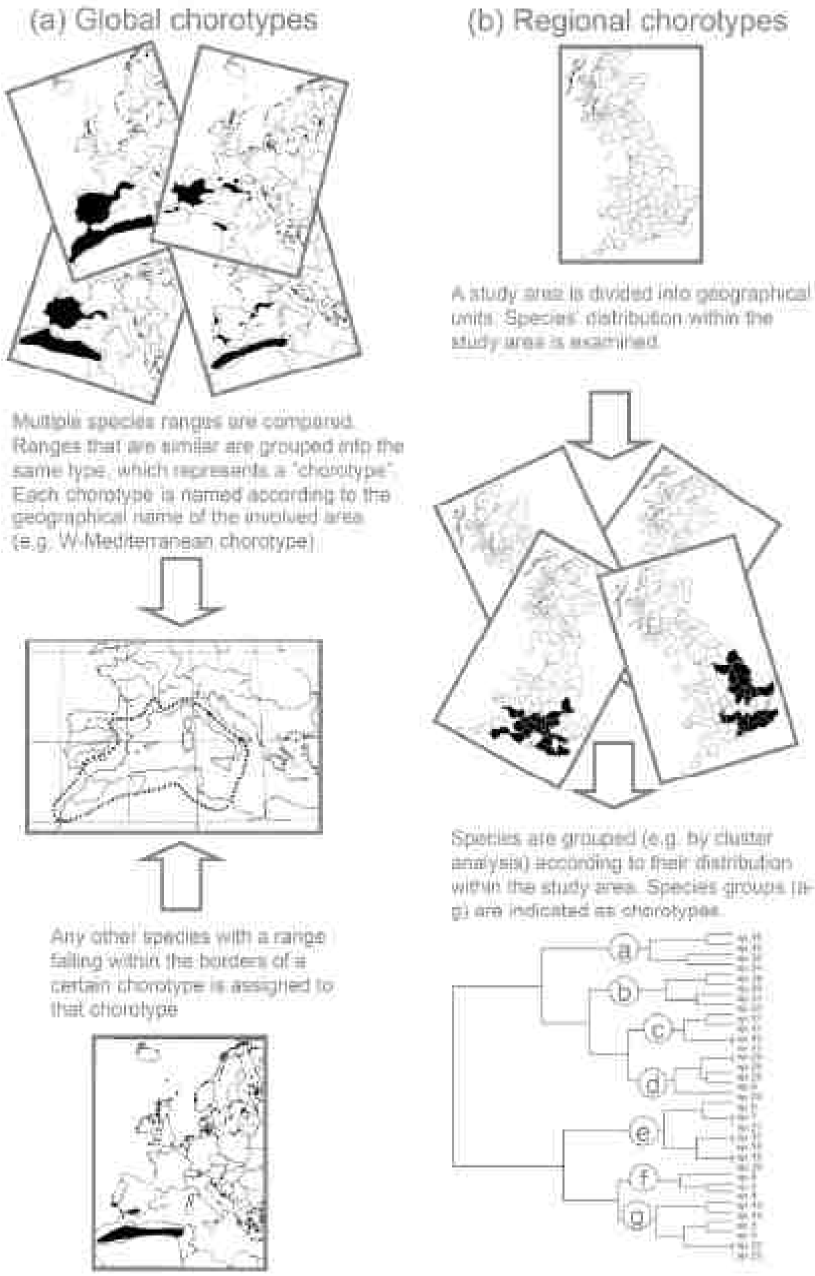

Figure 1 Diagramatic comparison between the concept of 'global chorotype' and 'regional chorotype' through fictional examples. To illustrate the concept of 'global chorotype' (panel a), a large number of species ranges (represented by the top set of maps showing the distribution of four butterfly species) is used to identify a recurrent type of distribution, i.e. a chorotype (in this case, the four species concur to define the

West Mediterranean chorotype, *sensu* Vigna Taglianti *et al.*, 1999). Any additional species with a similar range, is assigned to that chorotype (in this case, the species whose range is depicted in the map at the bottom). To illustrate the concept of regional chorotype (panel b), a study area (Great Britain) has been divided into geographical units (vice-counties). Then, the distribution of a hypothetical set of species is defined as presence/absence in the units included in the study area (as exemplified by a set of four maps where black units indicate areas occupied by the species). Cluster analysis is used to group species according to their distribution within the study area. Species grouped in the same cluster form a chorotype (in the example, 34 hypothetical species were grouped into seven clusters, a–g, recognized as distinct chorotypes).

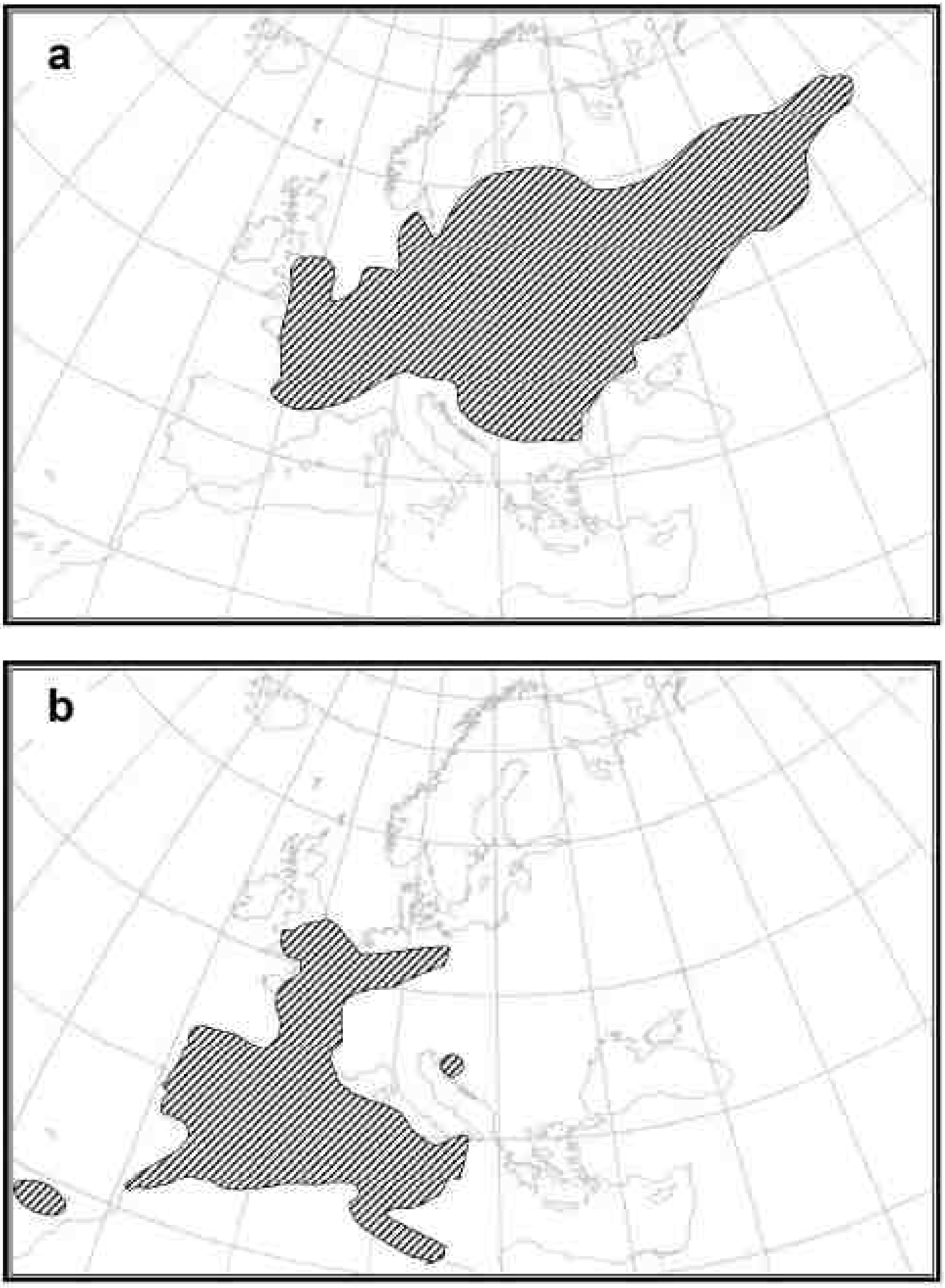

Figure 2 Two species of ground beetles (Coleoptera: Carabidae) with similar distribution in England, but very different ranges. Both species can be classified in the same regional chorotype (southern England), but *Agonum livens* (a) belongs to a Central European global chorotype whereas *Licinus punctatulus* (b) belongs to a Mediterranean global chorotype. Ranges are based on Seddon (1971) and updated according to Löbl &

Smetana (2003).