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RESEARCH PAPER

Using chorotypes to deconstruct biogeographical and biodiversity patterns: the case of breeding waterbirds in Europe

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ABSTRACT

Aim To deconstruct the biodiversity pattern of the 152 waterbird species breeding in Europe to better understand its multiple causal processes.

Location Continental Europe, Iceland and the British Isles.

Methods We considered the orders that are typically comprised by swimming, diving or wading birds, which inhabit marshes, fens, peatlands and fresh, brackish or salt waters, including coastal waters. We used the 55 main river basins of Europe as geographical units, and searched for either chorotypes (groups of similar species distributions) or gradual replacement of species throughout the river basins. Chorotypes were recognized by applying a probabilistic classification method to the distributions. Then we used GLM to characterize the extent and the species richness of each chorotype according to energy availability (higher levels of environmental energy favouring the presence of species), climatic stress due to an excess of energy, availability of water, productivity, seasonality and surface area.

Results One hundred and forty species significantly aggregate into nine chorotypes. The other 12 species, most of them marine, are centred on Great Britain, dropping away progressively on coasts further away from there. Differences in either the availability of energy or climatic stress significantly characterized the distribution of seven chorotypes comprising 90.8% of the species.

Main conclusions Chorotypes are meaningful and useful to deconstruct biodiversity patterns. Our results suggest that energy is the main factor related to the biogeographical patterns of breeding waterbirds in Europe, and provide an insight into regional trends of species richness previously analysed with a habitat-scale perspective.

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Keywords
Environmental energy, Europe, macroecology, river basins, species distribution, species richness, water availability.

INTRODUCTION

Marquet *et al.* (2004) proposed the deconstruction of biodiversity patterns according to the biological attributes of species as a way of gaining better insight into the causes of biogeographical trends. He used the word ‘deconstruction’ in its etymological sense, as a ‘turning to the roots’ of what is measured, or a ‘disaggregation’ to make apparent what is hidden. Certainly, as Huston (1994) also emphasized, it is useful to decompose biological diversity into components with consistent biogeographical responses to environmental conditions, and then analyse the processes, either historical or ecological, that influence each of them.

Baroni-Urbani *et al.* (1978) defined ‘chorotype’ as an elementary distribution pattern, followed by one or several species that can be operatively recognized within a territory. Chorotypes may result from ecological causes, i.e. differential responses to environmental conditions shared by several species, or from historical causes, i.e. past events that restricted or biased certain groups of species to different parts of the territory. The differential responses to the environment may have roots in the different regions of origin of the faunas, in which case the ecological cause

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would have a historical cause. Chorotypes may represent consistent biogeographical responses among subsets of species, and may thus be useful for deconstructing biodiversity and biogeographical patterns and in accounting for these patterns.

Waterbirds are a diverse group of species, from the taxonomical and morphological points of view, which share the ecological character of exploiting aquatic ecosystems. Wetlands form complex ecological systems where individual species differ in their use of the local wet environments. The variety of wetland types and their broad-scale distribution result in complex biogeographical trends for waterbirds. This is the kind of complex system for which properties are impossible to derive from the analysis of each individual species (Gaston & Blackburn, 1999). Conversely, the analysis of all species together may provide a blurry view of the overall distribution pattern. Finding common characteristics in the distribution of subsets of waterbird species may be useful for understanding the environmental influences on waterbirds as a whole.

The present configuration of broad-scale waterbird distribution in Europe is the result of historical processes probably related to the Pleistocene glaciations, which caused deep changes in climatic and environmental zones, and the modification of plant and animal dispersal routes (Lomolino *et al.*, 2006, p. 287). On the other hand, current climate, and especially the availability of water and energy, is considered by many authors to be a main macroenvironmental cause of large-scale biogeographical patterns (Currie, 1991; H-Acevedo & Currie, 2003; Hawkins *et al.*, 2003a). The availability of energy has been related to regional changes in waterbird species composition in Europe (Olivero *et al.*, 1998) and to geographical trends in bird species richness elsewhere (Turner *et al.*, 1988; Forsman & Mönkkonen, 2003), including European waterbirds (Bárcena *et al.*, 2004). The availability of water has been related to the biogeographical patterns of waterbirds in Africa (Guillet & Crowe, 1985) and in Australia (Whitehead *et al.*, 1992).

In this paper we analyse the chorotypes of breeding waterbird species in European river basins, and characterize their distribution patterns according to the current availability of water, environmental energy, productivity, seasonality and basin surface area to infer both their origins and the trends of biogeographically decomposed species richness. We also discuss the role of history and the geographical context in the definition of the current distribution patterns detected.

METHODS

The species and the study area

We analysed the breeding distribution of 152 indigenous waterbird species in continental Europe, the British Isles and Iceland. We included orders that are typically comprised by swimming, diving or wading birds, which inhabit marshes, fens, peatlands and fresh, brackish or salt waters, including coastal waters, and considered as coastal distributions those on islands up to 1 km from the coast. Species belonging to orders not typically dependent on wetlands, such as the orders Falconiformes, Coraciiformes and Passeriformes, were not considered.

The distributions of the species were obtained by compiling those appearing in Cramp & Simmons (1980a,b, 1983), Cramp (1985), Hagemeijer & Blair (1997) and 18 regional and local atlases (see Olivero *et al.*, 1998). We compiled the species occurrences in the 55 main river basins of Europe (see Olivero *et al.*, 1998 and Bárcena *et al.*, 2004).

River basins were used as geographical units because the topography, water availability and evapotranspiration of basins strongly affect the interchange of water, sediments, energy and nutrients among wetlands (Real *et al.*, 1993; Tucker & Evans, 1997). River basins also influence the nutrient enrichment of coastal waters near the river mouths (Mann & Lazier, 1991), thus affecting the birds breeding along or near the coast (Hay, 1992). In this way, basins are natural domains representing a level of ecosystem integration (Austin & Margules, 1986), especially suitable for studies in which the ecosystems involved are wetlands.

Probabilistic classification analysis to recognize chorotypes

Real *et al.* (1992b) developed a probabilistic procedure for recognizing chorotypes (see also Real *et al.*, 1997; Márquez *et al.*, 1997; Muñoz *et al.*, 2003). Following this procedure, we obtained a matrix of geographical similarities between the distributions of each pair of species (*a* and *b*) using Baroni-Urbani & Buser's (1976) index

$$\mathrm{SI} = \frac{\sqrt{(C \times D)} + C}{\sqrt{(C \times D)} + A + B - C}$$

where A is the number of basins in which the species a is present, B is the number of basins in which the species b is present, C is the number of basins where both species a and b are present together and D is the number of basins from which both species a and b are absent. A similarity value of 1 means completely coinciding distributions, and 0 means completely non-coinciding distributions. This coefficient takes into account shared absences, that is, European basins outside the distribution area of both species, and so the similarities were considered in the context of Europe (Real *et al.*, 1992a). Shared absences are important because they could be due to reasons of ecology or history that should be taken into account (Baroni-Urbani & Buser, 1976). However, this index gives more importance to shared presences, and the possibility that two distributions are considered similar only because of their shared absences is avoided by multiplying shared absences by shared presences.

The grouping of waterbird distributions was made using an agglomerative method of classification to maximize similarity within groups, a requisite of chorotypes. We used the unweighted pair-group method using arithmetic averages (UPGMA) because it produces the least distortion in relation to the original similarities between distributions (Sneath & Sokal, 1973), and expressed the result as a dendrogram.

We used the table of critical values in Baroni-Urbani & Buser (1976) to perform exact randomization tests (Sokal & Rohlf, 1981, p. 788) where the observed similarity values were compared with all the possible outcomes (see also Real & Vargas, 1996).

Values of the similarity index higher than 95% of outcomes were considered significant similarities (+), values lower than 95% of outcomes were significant dissimilarities (–) and the rest were considered values expected at random (Real *et al.*, 1992b; Márquez *et al.*, 1997).

To detect chorotypes, we explored all clusters of distributions in the dendrogram and selected those that combined the following characteristics: a high proportion of significant similarities (+) within the cluster, a low proportion of significant dissimilarities (–) within the cluster and a low proportion of significant similarities (+) between the distributions of the cluster and the distributions of the most similar cluster. The degree to which a cluster combines these conditions is provided by the internal homogeneity parameter (IH). For the mathematical expansion of this parameter, see 'DW(A×A)' in Márquez *et al.* (1997) and Vargas *et al.* (1997). We rescaled IH values to make them range between –1 and +1. In this way, we computed the IH values for every branch of the dendrogram. A cluster was considered a chorotype if: (1) IH = 1 or (2) IH was positive, was higher than those of the other clusters including the distributions involved and the proportion of signs '+' between the cluster and the most similar cluster was significantly lower than the proportion of signs '+' within the cluster (tested using a *G*-test of independence, Sokal & Rohlf, 1981). Distributions that did not fulfil these conditions did not constitute any chorotype, and so were considered as following a more gradual than discrete spatial pattern.

Environmental characterization of the chorotypes

We characterized the chorotypes using 10 variables related to one geographical and five climatic factors.

Availability of energy

Some species may need high values of environmental energy to satisfy their physiological requirements and to maintain their competitive capacity (Hutchinson, 1959; Wright, 1983; Currie, 1991). Positive relationships between the chorotype and mean annual temperature (*T*), mean temperature of July (Jul*T*), potential evapotranspiration (PET) or absolute potential evapotranspiration (APET) are indicators of the influence of this climatic factor. The APET is the result of multiplying PET by the area of the corresponding river basin, and so indicates the total energy available in a basin.

Climatic stress

A warm climate may cause physiological stress to some species whose chicks develop their thermoregulation early in life (Beintema & Visser, 1989). The influence of this factor can be deduced from a negative relationship between the chorotype and *T*, Jul*T* and PET.

Availability of water

Availability of water may be important in accounting for the continental distributions of waterbirds by providing suitable habitats (Guillet & Crowe, 1985; Whitehead *et al.*, 1992) and for their coastal distributions, since the run-off of rivers towards the sea may supply nutrients and so affect the coastal productivity (Mann & Lazier, 1991). A relationship of the chorotype and mean annual precipitation (*P*) is predicted.

Productivity

Differences in productivity between river basins may affect the distribution of species by conditioning food availability (Hawkins *et al.*, 2003b), thus supporting species using different parts of the food gradient. The simultaneous availability of water and energy, measured by actual evapotranspiration (AET) and absolute actual evapotranspiration (AAET), is a good indicator of productivity (Rosenzweig, 1968; Wright, 1983). The AAET is the result of multiplying AET by the area of the corresponding river basin, and so indicates the total productivity in a basin.

Seasonality

Seasonal blooms of prey increase the availability of food in climatically unstable environments with short summer growing seasons and harsh winters, thus allowing more species to exploit these environments during the breeding season (Herrera, 1978). We predicted a breeding chorotype related to this factor to have a positive relationship with the annual temperature range (TR) or a negative relationship with the mean temperature of January (Jan*T*).

Surface area

Basins with a greater area (*A*) may support more species than smaller ones (Arrhenius, 1921; Connor & McCoy, 1979). By considering this variable, we controlled the possibility that species were associated in chorotypes only because of their higher probability of occurring in river basins with higher surface areas.

We obtained *P*, *T* and Jul*T* values from the World Meteorological Organization (1970), PET and AET from the maps of the USSR National Committee for the International Hydrological Decade (1977) and *A* from Bartholomew *et al.* (1988).

We first searched for environmental differences between the river basins supporting at least one species of the chorotype and the rest of Europe. In this way we inferred the environmental conditions that may have limited the distribution of the whole set of species, which are probably related to the causes that originated the chorotype. We performed forward stepwise logistic regressions of the presence or absence of the chorotype in each basin on the above-mentioned variables. The statistical significance of the model was evaluated using a χ^2 test, and the estimation of the parameters in the logistic function was by maximum likelihood. The significance of the variables within the model was tested using the log-likelihood ratio (LR) criterion. Unimodal responses of the species to the environmental factors are possible if an intermediate range of environmental conditions is more suitable for the physiological requirements of the species included in a chorotype. To take into account these possible

Table 1 Values of IH (internal homogeneity parameter) for the tree branches in Fig. 1.

Cluster	IH
Chorotype 1	0.727*
Puffinus yelkouan and *Vanellus spinosus*	0.967 (n.s.)
Chorotype 2	0.823*
Chorotype 3	0.797*
Chorotype 4	0.729*
Chorotype 5	0.641*
Chorotype 6	0.667*
Chorotype 7	1.000
Chorotype 8	1.000
Chorotype 9	0.861*
Puffinus puffinus to *Oceanodroma leucorhoa*	0.627 (IHL)

*Significant *G*-tests of independence ($P < 0.001$).
n.s., non-significant *G*-tests of independence ($P \geq 0.05$).
IHL, IH value lower than those of other clusters including the distributions involved.

unimodal responses, for each chorotype we performed a logistic regression on each variable and its square. If a unimodal response was obtained, then we used the quadratic predictor as a new variable, in conjunction with the original ones, to be considered in the stepwise procedure that drives the final logistic regression model.

Second, we used the chorotypes to deconstruct the breeding waterbird diversity, and analysed the response of the species richness of each chorotype to the environmental conditions of the river basins where they occur. These deconstructed trends in species richness could be responsible for the maintenance of the chorotypes. We used the following logistic model:

$$S = \frac{\text{Min} + \text{Max} \times e^{Y}}{1 + e^{Y}}$$

where *S* is the species number of the chorotype present in each river basin, Min and Max are the minimum and the maximum, respectively, to which the function theoretically tends and *Y* is a regression equation as follows:

$$Y = a + bx_1 + cx_2 + \ldots + nx_n.$$

The variables $x_1 \ldots x_n$ and the initial values of the parameters *a*, *b*, *c* ... *n* used to adjust the logistic model were estimated by stepwise multiple regression of the variable $Y1 = \ln[(S - m)/(M - S)]$ on the environmental variables, where *S* is the species number of the chorotype observed in each basin, *M* is 1 plus the maximum number of species of the chorotype observed in one basin and *m* is the minimum number of species observed minus 1. The initial values for Min and Max were *m* and *M*, respectively. We took into account possible unimodal responses of species to the environmental factors in an analogous way as with the logistic regressions.

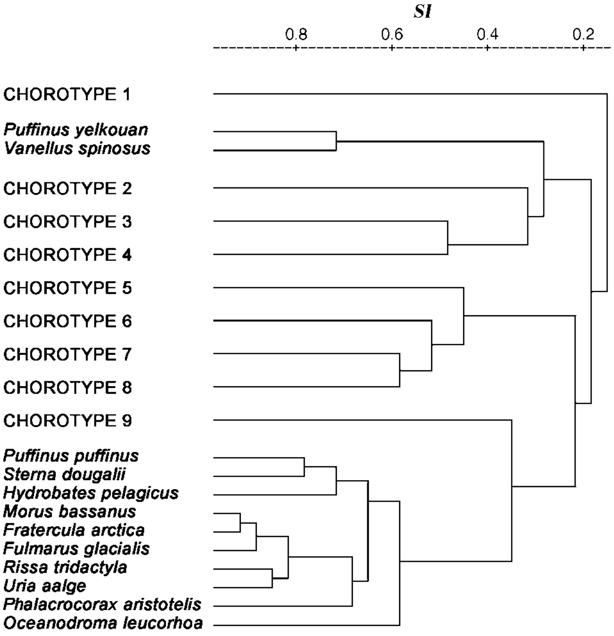

Figure 1 Classification tree derived from the UPGMA dendrogram. Only the branches corresponding to chorotypes and to species that do not belong to or constitute chorotypes are shown. SI, Baroni-Urbani & Buser similarity index (range 0–1).

RESULTS

We identified nine chorotypes for breeding waterbirds in Europe (Table 1; Figs 1–3; Appendix 1), which involve 140 species. Ten of the 12 species left are biogeographically related (see Fig. 1) marine species that seem to follow a gradually nested spatial pattern, with the core breeding distribution located on the coasts of Great Britain, and gradually diminishing breeding presences on most of the other European coasts (Table 2, Fig. 4).

About 70% of the species belong to chorotypes 3, 5 or 6, which are widespread but differ in tendency (see Fig. 2). Chorotype 3 is biased southward, because it is spread mostly below the 60° N parallel, and the highest concentration of these species occur in the mouth of the Guadalquivir (southern Spain) and of the main rivers that flow to the Mediterranean, Black and Caspian seas. Chorotype 5 presents a latitudinally unimodal response, with the lowest number of species in the Mediterranean peninsulas. Chorotype 6 is biased northward, since only a few species are present below the 50° N parallel.

The other chorotypes are geographically more restricted (Fig. 3). Chorotypes 1 and 9 are constrained to northern Europe, the first in the continent and the second mainly in Iceland. Chorotype 2 includes the most meridional, basically Iberian, distributions, while chorotype 4 is typically south-eastern. Chorotypes 7 and 8 are one-species chorotypes, namely *Xenus cinereus*, widespread along the Russia coast, and *Sterna caspia*, whose European breeding sites are mainly on the coasts of the Baltic, Caspian and Black seas.

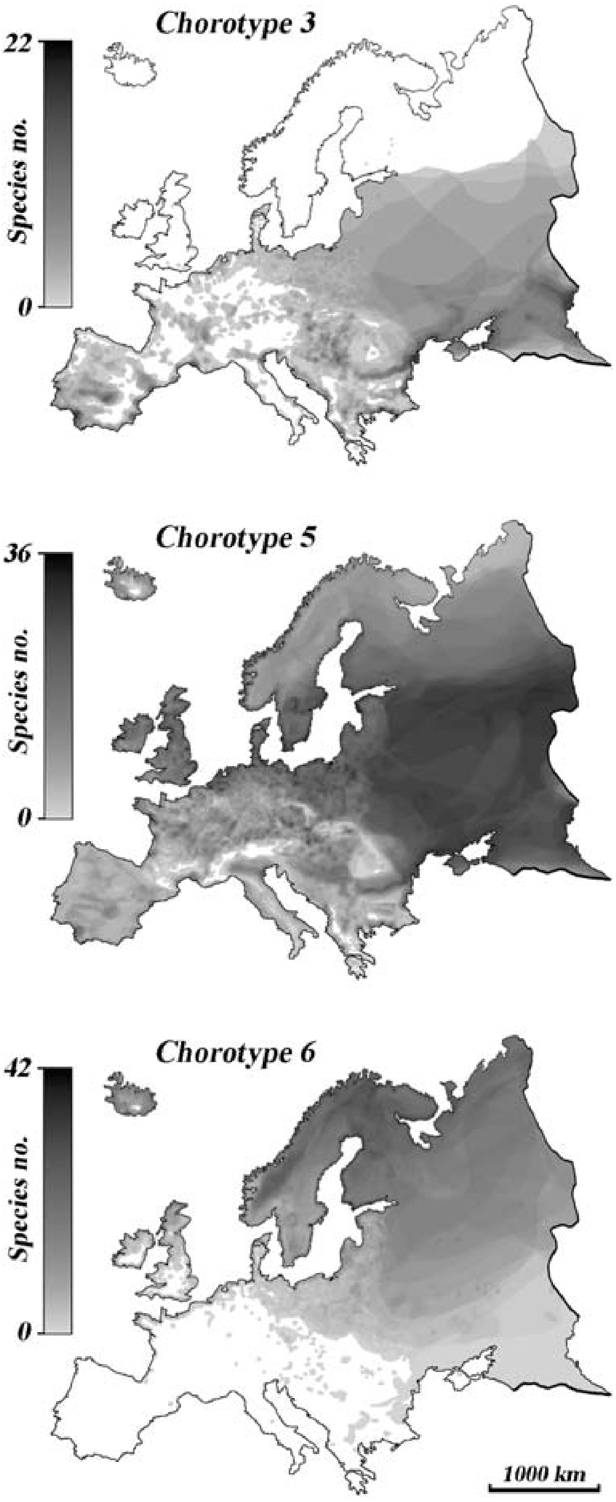

Figure 2 Geographical representation of the three 'widespread' chorotypes described in Europe for the breeding waterbirds, resulting from overlapping the distributions of the species comprising each chorotype. These species are listed in Appendix 1.

Table 2 Marine species that seem to follow a gradual spatial pattern, and their presence as breeders within the study area (indicated by X) (GB, Great Britain; Ir-nF, Ireland and northern France; Ic, Iceland; N, Norway; Ib, Iberian Peninsula; Fe, Fennoscandia out of Norway; M, Mediterranean sea out of the Iberian Peninsula; B, Black Sea) and world-wide (Eu, Europe and related islands; EC, eastern Canada; Gr, Greenland; WC, western Canada; A, Alaska; WU, west USA; EA, east Asia; W, world-wide).

	GB	Ir-nF	Ic	N	Ib	Fe	M	B
Oceanodroma leucorhoa	X		X					
Puffinus puffinus	X	X						
Sterna dougalii	X	X			X			
Hydrobates pelagicus	X	X	X		X		X	
Morus bassanus	X	X	X	X				
Fratercula arctica	X	X	X	X				
Fulmarus glacialis	X	X	X	X				
Uria aalge	X	X	X	X	X	X		
Rissa tridáctilas	X	X	X	X	X	X		
Phalacrocorax aristotelis	X	X	X	X	X	X	X	X

	Eu	EC	Gr	WC	A	WU	EA	W
Phalacrocorax aristotelis	X							
Hydrobates pelagicus	X							
Morus bassanus	X	X						
Puffinus puffinus	X	X						
Fratercula arctica	X	X	X					
Fulmarus glacialis	X	X	X	X	X	X		
Rissa tridáctilas	X	X	X	X	X	X		
Oceanodroma leucorhoa	X	X		X	X	X	X	
Uria aalge	X	X	X	X	X	X	X	
Sterna dougalii	X	X	X	X	X	X	X	X

Productivity, surface area and availability of water seem to be only marginal explanatory factors for the chorotypes. Only the species number of chorotype 3 has been characterized, secondarily, by the productivity of the basins (Table 3). The surface area of the basins only is a secondary factor to account for the origin of chorotypes 2 and 7 (Table 3). Water availability only is a secondary factor accounting for the species number of chorotypes 3 and 5, and in both cases the availability of water is low in the basins occupied by the chorotypes (Table 3).

In contrast, climatic stress and energy availability are the main explanatory factors accounting for the origin and the species number of seven chorotypes, involving 90.8% of the species (Table 3). Climatic stress (due to an excess of energy) is the most important factor explaining the origins of chorotypes 1, 6 and 9, with 39.5% of the species; energy availability is the most important factor involved in the origin of chorotypes 2, 3 and 4, with 27.6% of the species. For the trends in species richness, the most important factors are climatic stress for chorotypes 1, 6 and 9 (39.5% of the species), availability of energy for chorotype 4 (8.6% of the species) and both climatic stress and availability of energy for chorotypes 3 and 5 (38.2% of the species).

Seasonality is the main factor to explain the origin of the unispecific chorotypes 7 and 8, and a secondary factor for the origin of chorotype 4 and for the trend in species richness of chorotype 3.

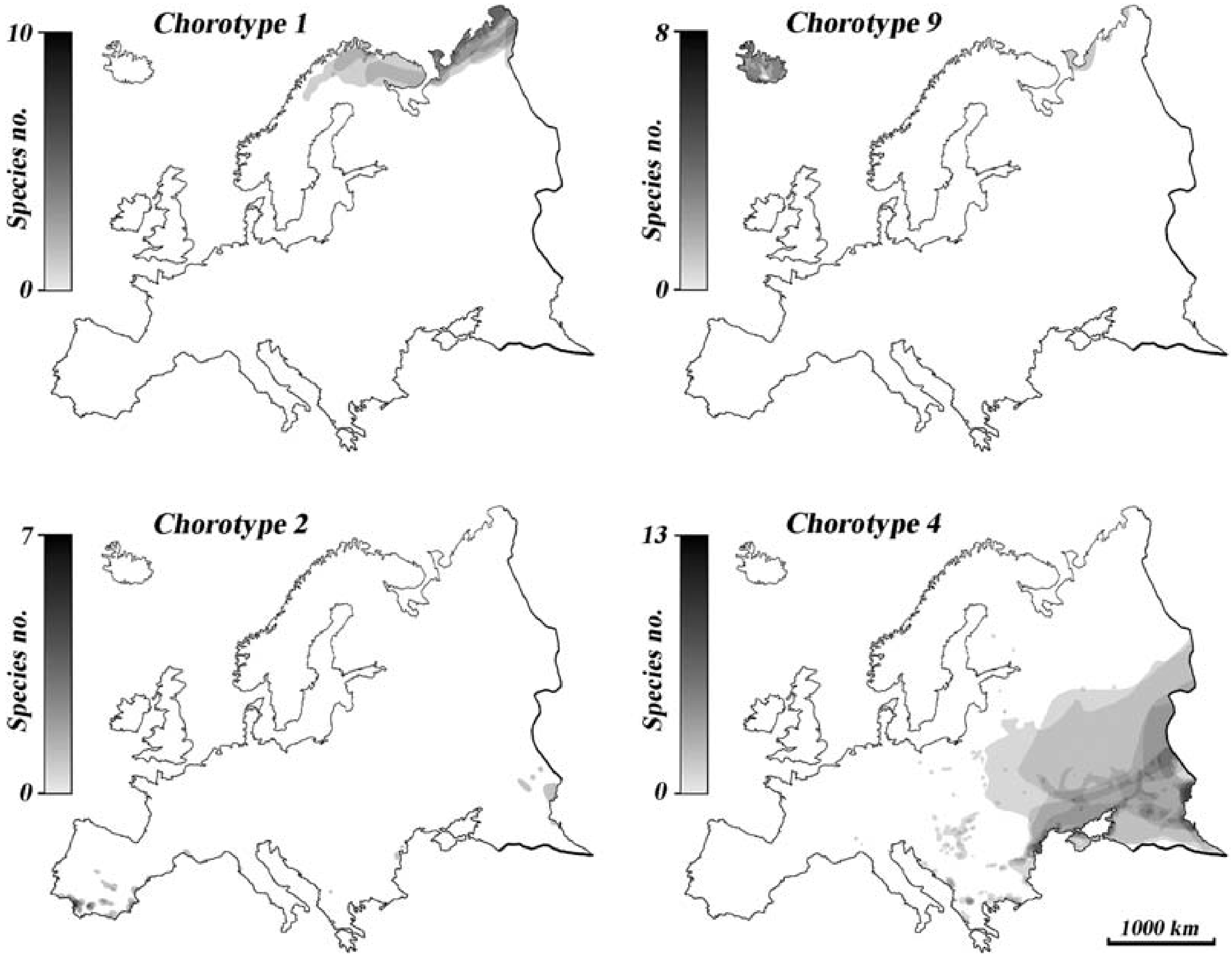

Figure 3 Geographical representation of the three 'geographically restricted' chorotypes described in Europe for the breeding waterbirds, resulting from overlapping the distributions of the species comprising each chorotype. These species are listed in Appendix 1.

DISCUSSION

Historical and regional context of the European chorotypes of breeding waterbirds

The scarcity of birds with relatively small geographical ranges in Europe could have been the result of the relatively recent effects of the Quaternary glaciations on bird species, compounded with the spatial configuration of the European geographical barriers. Probably only bird species with good dispersal capabilities, normally with large geographical ranges, could survive the glaciers and severe swings in climatic conditions during the Quaternary, whereas geographically restricted species, with more limited dispersal abilities, could not escape (Lomolino *et al.*, 2006, p. 580). Even in the Mediterranean peninsulas, species with low dispersal capabilities may have been subjected to more severe interspecific competition in the smaller, and probably drier, available areas, with the resulting elimination of some species. This, and the high mobility of waterbirds compared with some terrestrial birds, suggests a historical explanation for why 70% of breeding waterbirds in Europe are included in the three widespread chorotypes 3, 5 and 6. However, the varied world-wide distribution of the species included in them makes it difficult to interpret the origins of these three chorotypes on the basis of differential historical causes.

The chorotypes that are geographically more restricted in Europe contain species that are widespread at the global scale. These chorotypes occur at the fringes of the continent, where they seem to represent the westernmost or easternmost extremes of wider distribution areas. Consequently these restricted chorotypes may be historically related to external source areas, and may be partially caused by proximity to them. The oriental chorotype 4 is probably related to the steppes of central Asia, where all the species of this chorotype are found, although half the species also breed in areas of southern and eastern Asia, central Africa, North and South America and Australia. The steppe species of this chorotype may have occurred in the south-east of Europe also during the glaciations, because this biome remained there during the Würm glacial maximum, 18,000 years ago (Lomolino *et al.*, 2006, p. 290). The species of chorotype 1 are all present in the Russian tundra, with most of them also breeding in northern North America and some of them in

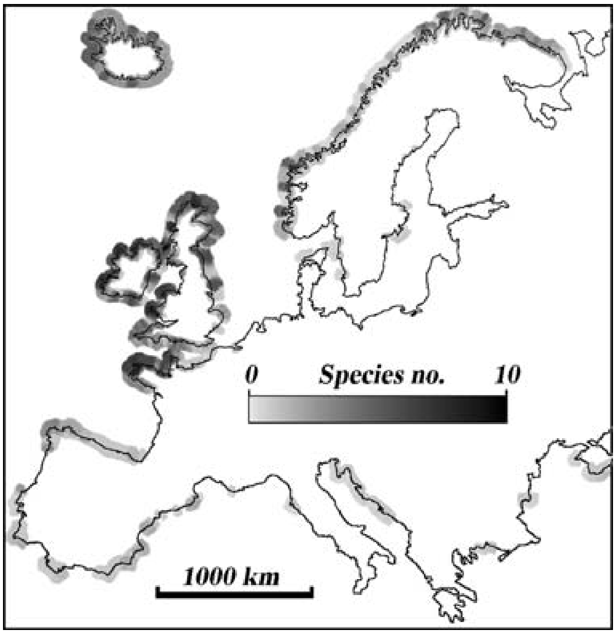

Figure 4 Overlap of the continental European distribution of the 10 marine species that seem to follow a gradual pattern of spatial substitutions. These species are listed in Table 2. Shading is projected seaward for visibility.

Greenland. Although these northern species seem to have originated in the east, they might have had wider distributions in Europe during the glaciations, when the tundra occupied most of the continent from the ice limits to the interior of the Mediterranean peninsulas (Lomolino *et al.*, 2006, p. 290). On the contrary, the northern chorotype 9 contains Nearctic species that might have colonized recently from North America via Greenland. However, the species of chorotype 2 have diverse global ranges, with three species more or less restricted to the Mediterranean context, two with extensive breeding distributions in central Asia and two species reaching central and southern Asia, Africa and Australia. Consequently, the origin of this chorotype is not likely to be the result of a shared history.

The meaning of chorotypes

The shared spatial responses presented by the majority of breeding waterbirds in Europe are mainly attributable to ecological processes. This is in agreement with Passerin D'Entrèves & Zunino (1992) and Zunino (2005), who suggested that a chorotype based on species distributions (which they called first-order chorotypes; see Bellucci *et al.*, in press) should be mainly interpreted using the ecological links between the species, whereas chorotypes based on monophyletic supraspecific taxa (second-order chorotypes; see Bellucci *et al*, in press) are more appropriate to generate hypotheses related to the biogeographical history.

Since chorotypes are defined here for large geographical units (river basins) that include many wetland types, they are not ecological assemblages of species, but rather reflect a large spatial pattern that is probably ruled by macroecological factors. In this way, a chorotype usually consists of species that do not share a habitat or way of life (e.g. seabirds can share a chorotype with freshwater birds; see Appendix 1). Conversely, species of different chorotypes could belong to the same waterbird community in a given wetland. Chorotypes merit some consideration from the point of view of conservation biogeography. The effects of macroenvironmental factors, such as global warming, on bird distributions may not only affect the species individually but also disrupt the overlapping of their distributions and the complex interrelationships that may be favoured by their co-occurrence. Lomolino (2004) pointed out that to conserve species, it is necessary to conserve their distributions, which constitute their geographical, ecological and evolutionary context. We could analogously argue that chorotypes should be also preserved, as they represent the shared geographical, ecological and evolutionary context of several species.

As chorotypes may overlap, each species could be defined as having a degree of membership in the different chorotypes described. In this sense, the distributions included in a chorotype constitute a group that is fuzzy by nature, so that the principles

Table 3 Variables selected in the environmental characterization of the origin of chorotypes and their species number. We indicate whether the variables have monotonic (mon) or unimodal (unim) and positive (pos) or negative (neg) relations with the chorotype, and point out the environmental factors involved.

Chorotype	Origin characterization	Species number characterization
1	PET (mon, neg) stress Jul$T$ (mon, pos) energy	PET (mon, neg) stress
2	PET (mon, pos) energy A (mon, pos) surface	n.s.
3	PET (mon, pos) energy	PET (unim) energy and stress TR (mon, pos) seasonality T (mon, pos) energy AAET (mon, pos) productivity P (mon, neg) water
4	PET (mon, pos) energy TR (unim) seasonality APET (mon, pos) energy	APET (mon, pos) energy
5	Not applicable	PET (unim) energy and stress T (unim) energy and stress P (mon, neg) water
6	PET (mon, neg) stress	T (mon, neg) stress PET (mon, neg) stress
7	TR (mon, pos) seasonality A (mon, pos) surface Jul$T$ (unim) energy and stress	Not applicable
8	TR (mon, pos) seasonality	Not applicable
9	Jul$T$ (mon, neg) stress	Jul$T$ (mon, neg) stress

n.s., no significant model found.
A, surface area; AAET, absolute actual evapotranspiration; AET, actual evapotranspiration; APET, absolute potential evapotranspiration; Jan$T$, mean temperature of January; Jul$T$, mean temperature of July; P, mean annual precipitation; PET, potential evapotranspiration; T, mean annual temperature; TR, temperature range.

and rules of fuzzy logic may be easily applied to them. In addition, a correct interpretation of chorotypes must take into account that they are susceptible to changing over time, and that the perception of them also changes with the type of geographical unit analysed, the scale and the set of species included in the analysis. A quantification of the fuzziness of chorotypes might predict to some degree these possible modifications, because fuzzier chorotypes may be more susceptible to change.

Chorotypes are also good biodiversity decomposers, in the sense of Marquet *et al.* (2004). Although Bárcena *et al.* (2004) showed, for example, that energy plays the main role in shaping the latitudinal trends in waterbird species richness in Europe, our deconstruction according to chorotypes allowed us to analyse in more detail the causes of their biogeographical trends.

Seabirds and the gradual distribution pattern

The 10 marine species that follow a gradually nested distribution pattern also follow a gradually nested pattern if we examine their world-wide ranges (see Table 2). Coastal breeding distributions of marine waterbirds may follow a pattern that is ruled by oceanic parameters, which presumably vary more gradually than continental ones. Olivero *et al.* (1998) found that winter coastal distributions of seabirds were related to water run-off in nearby continental areas. In winter, blending winds delay stratification, and so the increase in productivity due to river plumes is maintained close to the coast (Mann & Lazier, 1991). In spring, the offshore burst of productivity is mainly caused by broad-scale water stratification deriving from surface warming, and migrates from the coast to deeper waters as the season progresses (Mann & Lazier, 1991). Oceanic blooms that occur far from the coast during springtime could affect the breeding distribution of seabirds distantly and, thus, gradually. The pelagic distribution of seabirds in the breeding season also seems to lack significantly joined occurrences, as has been shown by Veit (1995) for most seabird species in a broad-scale analysis in the South Atlantic Ocean.

The roles of water and energy in the characterization of chorotypes

Availability of energy and climatic stress due to an excess of energy were the environmental factors that characterized most of the chorotypes detected. This is in agreement with the results of Olivero *et al.* (1998), who found that energy, rather than water, best accounted for the biotic boundaries and regions obtained according to breeding waterbird distribution in the European river basins. Forsman & Mönkkonen (2003) also suggested that temperature, more than precipitation, is the climatic gradient along which resident terrestrial bird densities varied most strongly in Europe.

However, in Africa (Guillet & Crowe, 1985) and Australia (Whitehead *et al.*, 1992), rainfall has been shown to be the most important factor governing bird regionalization. Olivero *et al.* (1998) suggested that water availability is probably a more important factor than energy for birds in Africa and in Australia because the range of rainfall within these continents is very high (from tropical to desert rainfall regimes). In Europe, although the absolute range of rainfall is nearly as high as in Australia or Africa, extreme values are recorded at very local sites. Our results suggest that, at the river basin scale, low precipitation and high evapotranspiration levels that occur locally in some parts of the south and east of Europe do not cause water availability to be an important limiting factor for waterbirds. Waterbirds mainly concentrate around wetlands, and these water-sustained ecosystems exist, with diverse configurations, even in the drier European basins. This scenario might change, however, if the predicted global warming has the impact of drying out the Mediterranean region.

Hawkins *et al.* (2003b), found that environmental energy best predicts the diversity gradient of terrestrial birds at high latitudes, whereas water-related variables best predict richness in low-latitude, high-energy regions. Our results suggest that this statement could be extended to waterbirds, and that Europe would be at a latitudinal range where species richness can still be best predicted by environmental energy.

The effect of seasonality

In Europe, seasonality has been postulated as a main factor to explain the richness of aestival (non-resident breeding) waterbird species (Bárcena *et al.*, 2004), as climatic seasonality causes great availability of resources in the breeding season but at the same time the scarcity of resources in the non-breeding season may impose high mortality on resident species. Since 84% of the breeding waterbird species in Europe have aestival populations, we could expect seasonality to be one of the most important factors associated with the breeding chorotypes, particularly for those located in the north where seasonality is most pronounced. The environmental analysis of our chorotypes, however, does not indicate a significant effect of seasonality on the northern chorotypes 1, 6 and 9. Notwithstanding this, in chorotype 1 the combination of high values of Jul*T* with low values of PET indicates the basins, among those with the lowest annual PET, that have the highest temperature in July. These are cold areas with relatively warm summers where there is a summer bloom of resources.

Seasonality is more clearly involved in the environmental characterization of chorotypes 4 (south-eastern), 7 (Russian) and 8 (south-eastern and Fennoscandian), and is a secondary factor accounting for the species richness of chorotype 3 (widespread, but biased to the east), all of which have a strong 'eastern component'. This might indicate that in Europe, for breeding waterbirds, seasonality is more important for explaining the longitudinal than the latitudinal pattern.

Availability of energy and climatic stress

Environmental energy has been customarily considered as positively related to broad-scale species richness (see, for instance, Currie, 1991). However, the prevalence of negative relations between chorotypes (with 39.5% of the species) and energy variables, suggests that the existence of an environmental stress on breeding waterbirds due to high energy in the south is also a consistent hypothesis, as suggested by Bárcena *et al.* (2004). Should climate evolve as predicted by the IPCC, global warming could imply a northward displacement of chorotypes 1, 6 and 9, characterized by climatic stress, a southward spread of chorotype 4, characterized by the availability of energy, and a geographical adjustment of chorotypes 3 and 5, characterized by both factors. These changes could even prevent species of chorotype 1, now restricted to a narrow Arctic strip, from breeding in Europe.

Some geographical trends, such as those shown by Scolopacidae and Charadriidae throughout Europe, have been previously related to the availability of energy and climatic stress. Olivero *et al.* (1998) found that Scolopacidae are biased to the northern biotic regions defined for waterbirds, whereas Charadiidae are biased to the southern biotic regions. Beintema & Visser (1989) proposed that the earlier development of thermoregulation in the Scolopacidae may be related to their more northerly distribution with respect to the Charadriidae, because earlier development of thermoregulation implies a higher energy intake and a high metabolic rate which can cause environmental stress in warm weather (see also Koskimies & Lahti, 1964). The analysis of chorotypes is congruent with this environmental explanation: in Europe, the ratio of Charadriidae/Scolopacidae species is 2/5, but in the chorotypes that are mainly characterized by climatic stress, this ratio is lower (1/3 in chorotype 1, 1/5 in chorotype 6, and 0/1 in chorotype 9), in the chorotypes mainly characterized by the availability of energy, the ratio is higher (2/1 in chorotype 4), whereas in chorotype 5, characterized by both climatic stress and the availability of energy, the ratio is exactly 2/5.

Chorotypes as biodiversity deconstruction tools

Our deconstruction of broad-scale biodiversity patterns could also provide insights into regional trends of species richness previously analysed with a habitat-scale perspective. For example, in Finland the species number of waders has been reported to decrease southward, with twelve species breeding only in the north, six breeding only in the south and seven latitudinally widespread (Järvinen & Sammalisto, 1976; Järvinen & Väisänen, 1978; Boström & Nilsson, 1983; Järvinen *et al.*, 1987). Different causes have been postulated to explain this trend: habitat heterogeneity plus wetland stability (Järvinen & Sammalisto, 1976); habitat heterogeneity (Järvinen & Väisänen, 1978); concentration of invertebrates plus availability of suitable habitats (Boström & Nilsson, 1983); availability of suitable habitats (Järvinen *et al.*, 1987). Chorotypes may help explain these patterns as the result of more general responses of waterbirds to environmental energy. Five of the six wader species with southern Finnish distribution belong to chorotype 5, whereas 11 of the 12 species with northern Finnish distribution belong to chorotype 6. Both chorotypes are widespread in Europe, but the species richness of chorotype 5 decreases in the north, where there is less energy available, whereas chorotype 6 is biased to the northern basins, where the climatic stress is lower. Chorotype 6 contains more wader species than chorotype 5, both in Finland and in Europe. The higher wader species richness in the north of Finland could derive from two biogeographical patterns for waders on the European scale resulting from two different responses of species to energy, one of which is followed by more wader species than the other. This illustrates that chorotypes seem to be useful for deconstructing biodiversity patterns in the way Marquet *et al.* (2004) suggested.

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BIOSKETCHES

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Appendix 1 Species included in the nine chorotypes.

Chorotype	Common name	Species name
B1	White-billed Diver	*Gavia adamsii*
	Bewick's Swan	*Cygnus columbianus*
	White-fronted Goose	*Anser albifrons*
	Lesser White-fronted Goose	*Anser erythropus*
	King Eider	*Somateria spectabilis*
	Grey plover	*Pluvialis squatarola*
	Little Stint	*Calidris minuta*
	Pintail Snipe	*Gallinago stenura*
	Bar-tailed Godwit	*Limosa lapponica*
	Pomarine Skua	*Stercorarius pomarinus*
B2	Cory's Shearwater	*Calonectris diomedea*
	Greater Flamingo	*Phoenicopterus roseus*
	Marbled Teal	*Marmaronetta angustirostris*
	White-headed Duck	*Oxyura leucocephala*
	Purple Swamphen	*Porphyrio porphyrio*
	Red-knobbed Coot	*Fulica cristata*
	Audouin's Gull	*Larus audouinii*
B3	Little Bittern	*Ixobrychus minutus*
	Black-crowned Night Heron	*Nycticorax nycticorax*
	Squacco Heron	*Ardeola ralloides*
	Cattle Egret	*Bubulcus ibis*
	Little Egret	*Egretta garzetta*
	Purple Heron	*Ardea purpurea*
	Black Stork	*Ciconia nigra*
	White Stork	*Ciconia ciconia*
	Common Spoonbill	*Platalea leucorodia*
	Red-crested Pochard	*Netta rufina*
	Ferruginous Duck	*Aythya nyroca*
	Little Crake	*Porzana parva*
	Baillon's Crake	*Porzana pusilla*
	Black-winged Stilt	*Himantopus himantopus*
	Pied Avocet	*Recurvirostra avosetta*
	Collared Pratincole	*Glareola pratincola*
	Kentish Plover	*Charadrius alexandrinus*
	Mediterranean Gull	*Larus melanocephalus*
	Slender-billed Gull	*Larus genei*
	Caspian Gull	*Larus cachinnans*
	Gull-billed Tern	*Gelochelidon nilotica*
	Whiskered Tern	*Chlidonias hybridu*
B4	Pygmy Cormorant	*Phalacrocorax pygmeus*
	Great White Pelican	*Pelecanus onocrotalus*
	Dalmatian Pelican	*Pelecanus crispus*
	Great White Egret	*Egretta alba*
	Glossy Ibis	*Plegadis falcinellus*
	Ruddy Shelduck	*Tadorna ferruginea*
	Demoiselle Crane	*Anthropoides virgo*
	Black-winged Pratincole	*Glareola nordmanni*
	Caspian Plover	*Charadrius asiaticus*
	Sociable Lapwing	*Vanellus gregarius*
	Marsh Sandpiper	*Tringa stagnatilis*
	Great Black-headed Gull	*Larus ichthyaetus*
	White-winged Black Tern	*Chlidonias leucopterus*
B5	Little Grebe	*Tachybaptus ruficollis*
	Great Crested Grebe	*Podiceps cristatus*
	Black-necked Grebe	*Podiceps nigricollis*
	Great Cormorant	*Phalacrocorax carbo*
	Great Bittern	*Botaurus stellaris*
	Grey Heron	*Ardea cinerea*
	Mute Swan	*Cygnus olor*
	Greylag Goose	*Anser anser*
	Common Shelduck	*Tadorna tadorna*
	Gadwall	*Anas strepera*
	Common Teal	*Anas crecca*
	Mallard	*Anas plathyrhynchos*
	Northern Pintail	*Anas acuta*
	Garganey	*Anas querquedula*
	Northern Shoveler	*Anas clypeata*
	Pochard	*Aythya ferina*
	Tufted Duck	*Aythya fuligula*
	Common Goosander	*Mergus merganser*
	Water Rail	*Rallus aquaticus*
	Spotted Crake	*Porzana porzana*
	Common Moorhen	*Gallinula chloropus*
	Eurasian Coot	*Fulica atra*
	Eurasian Oystercatcher	*Haematopus ostralegus*
	Little Ringed Plover	*Charadrius dubius*
	Northern Lapwing	*Vanellus vanellus*
	Common Snipe	*Gallinago gallinago*

Appendix 1 *Continued*

Chorotype	Common name	Species name
	Black-tailed Godwit	*Limosa limosa*
	Eurasian Curlew	*Numenius arquata*
	Common Redshank	*Tringa totanus*
	Common Sandpiper	*Actitis hypoleucos*
	Black-headed Gull	*Larus ridibundus*
	Common Gull	*Larus canus*
	Sandwich Tern	*Thalasseus sandvicensis*
	Common Tern	*Sterna hirundo*
	Little Tern	*Sternula albifrons*
	Black Tern	*Chlidonias niger*
B6	Red-throated Diver	*Gavia stellata*
	Black-throated Diver	*Gavia arctica*
	Red-necked Grebe	*Podiceps grisegena*
	Slavonian Grebe	*Podiceps auritus*
	Whooper Swan	*Cygnus cygnus*
	Bean Goose	*Anser fabalis*
	Eurasian Wigeon	*Anas penelope*
	Greater Scaup	*Aythya marila*
	Common Eider	*Somateria mollissima*
	Long-tailed Duck	*Clangula hyemalis*
	Common Scoter	*Melanitta nigra*
	Velvet Scoter	*Melanitta fusca*
	Common Goldeneye	*Bucephala clangula*
	Smew	*Mergus albellus*
	Red-breasted Merganser	*Mergus serrator*
	Common Crane	*Grus grus*
	Ringed Plover	*Charadrius hiaticula*
	Eurasian Dotterel	*Charadrius morinellus*
	Eurasian Golden Plover	*Pluvialis apricaria*
	Temminck's Stint	*Calidris temminckii*
	Purple Sandpiper	*Calidris maritima*
	Dunlin	*Calidris alpina*
	Broad-billed Sandpiper	*Limicola falcinellus*
	Ruff	*Philomachus pugnax*
	Jack Snipe	*Lymnocryptes minimus*
	Great Snipe	*Gallinago media*
	Whimbrel	*Numenius phaeopus*
	Spotted Redshank	*Tringa erythropus*
	Common Greenshank	*Tringa nebularia*
	Green Sandpiper	*Tringa ochropus*
	Wood Sandpiper	*Tringa glareola*
	Ruddy Turnstone	*Arenaria interpres*
	Red-necked Phalarope	*Phalaropus lobatus*
	Arctic Skua	*Stercorarius parasiticus*
	Long-tailed Skua	*Stercorarius longicaudus*
	Little Gull	*Larus minutus*
	Lesser Black-backed Gull	*Larus fuscus*
	Herring Gull	*Larus argentatus*
	Great Black-backed Gull	*Larus marinus*
	Arctic Tern	*Sterna paradisaea*
	Razorbill	*Alca torda*
	Black Guillemot	*Cepphus grylle*
B7	Terek Sandpiper	*Xenus cinereus*
B8	Caspian Tern	*Sterna caspia*
B9	Great Northern Diver	*Gavia immer*
	Pink-footed Goose	*Anser brachyrhynchus*
	Harlequin Duck	*Histrionicus histrionicus*
	Barrow's Goldeneye	*Bucephala islandica*
	Grey Phalarope	*Phalaropus fulicaria*
	Great Skua	*Stercorarius skua*
	Glaucous Gull	*Larus hyperboreus*
	Brünnich's Guillemot	*Uria lomvia*
Species that do not belong to or constitute chorotypes	Northern Fulmar	*Fulmaurus glacialis*
	Manx Shearwater	*Puffinus puffinus*
	Yelkouan Shearwater	*Puffinus yelkouan*
	European Storm-petrel	*Hydrobates pelagycus*
	Leach's Storm-petrel	*Oceanodroma leucorhoa*
	Northern Gannet	*Morus bassanus*
	Common Shag	*Phalacrocorax aristotelis*
	Spur-winged Lapwing	*Vanellus spinosus*
	Black-legged Kittiwake	*Rissa tridactiyla*
	Roseate Tern	*Sterna dougalii*
	Common Guillemot	*Uria aalge*
	Puffin	*Fratercula arctica*