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Distribution of breeding, wintering, and resident waterbirds in Europe: biotic regions and the macroclimate

Jesús Olivero, Raimundo Real & J. Mario Vargas

Olivero, J., Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, E-29071 Málaga, Spain. E-mail: jolivero@uma.es.
Real, R., Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, E-29071 Málaga, Spain. E-mail: rrgimenez@uma.es.
Vargas, J. M., Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, E-29071 Málaga, Spain. E-mail: jmvy@uma.es.

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We developed a new method of testing whether spatial change in species composition follows a gradual or discrete pattern. To do this, we first divided Europe into regions based on 55 river basins. We then tested similarity of waterbird species assemblages between river basins using presence/absence data, and classified the basins using a probabilistic analysis. Breeding, wintering and resident species were analyzed separately. Some hypotheses related to macroclimate were tested to account for the distribution of waterbird species composition of river basins, using stepwise logistic regression and canonical variate analysis. We detected a strong biotic boundary dividing Europe into large northern and southern regions in both the breeding and wintering seasons. These large regions were subsequently divided, mainly by longitudinal weak boundaries, into a total of six biotic regions for each season. A more fragmented pattern was detected for resident species: four large regions and a total of eight biotic regions. Variables related to temperature characterized the majority of biotic boundaries. Low energy availability of the northern basins in the wintering season may limit the distribution of many wintering species, whereas the higher energy level of the southern basins in the breeding season might cause thermoregulatory stress for many breeding species.

1. Introduction

The European distribution of almost all waterbird species is well known and biogeographical analyses of these species are relatively frequent. However, most of these studies are on a regional scale (e.g., Järvinen & Sammalisto 1976, Fox & Bell 1994) and mainly analyze the species richness of breeding waterbirds (e.g. Järvinen & Väisänen 1978, Elmberg et al. 1993). Hengeveld (1990) stated that broad-scale approaches should precede fine-scale ones, since knowledge of biogeographical patterns on a continental scale is an important reference for later studies on regional and local scales. In addition, most waterbirds are migratory, resulting in a cyclic reorganization of the species' distributions. Therefore, it is necessary to analyze biogeographical patterns of migratory birds in the wintering and breeding seasons separately. Some authors have considered that the distribution of resident birds may affect the biogeographical patterns of migrant birds (Herrera 1978, Timonen et al. 1994), so that it is also necessary to analyze patterns shown by resident waterbirds.

Margules (1986) noted that classifying geographical areas into groups with different species composition is necessary to ensure that all these groups are represented in the selection of natural reserves. Thus, the definition of biogeographical zones, used in conjunction with the list of characteristic species, provides a basis for assessing priorities for conservation (Carey et al. 1995). This is why a major goal of many biogeographical studies is to determine whether the land areas on different scales can usefully and meaningfully be divided into biotic regions. Operationally, this is the transformation of Operational Geographic Units (OGUs: any one of the set of geographic units to be analyzed in a study; Crovello 1981), delimited only by geographic boundaries, into Operational Biogeographic Units (OBUs: any subset of OGUs constituting a biotic region), which are delimited by biotic boundaries.

Methodologically, ordination techniques are more suitable for analyzing continuum patterns, whereas classification analysis is more suitable for discrete patterns (Hengeveld 1990, Real et al. 1997). However, Jackson et al. (1992) stated that both ordination and classification methods assume that species form structured ecological or biogeographical communities, but these methods do not allow to test these asumptions. In the present paper we applied the coefficient model proposed by Jackson et al. (1992) for detecting possible spatial discontinuities in the composition of breeding, wintering and resident waterbird assemblages in Europe. Our method consists of a classification of areas complemented by a probabilistic analysis in which the similarity values used in the classification analysis are tested against the values of the index expected at random (see Jackson et al. 1992).

To understand the relationship of environment with the biogeographical patterns observed, it is necessary to test different hypotheses about processes that may operate on a broad geographical scale. Studies about environmental influences on the distribution of waterbirds usually focus on water levels (e.g. David 1994) or other local characteristics of wetlands such as vegetation or habitat structure (e.g. Elmberg et al. 1994), using hypotheses that usually involve nest site availability, predation, competition, mortality or food abundance. Although the habitat selection may be explained by these factors (see, for example, Hildén, 1965), macroclimate may be the main factor accounting for biogeographical patterns on a broad scale (Hengeveld & Hogeweg 1979, Wiens 1989, Sætersdal & Birks 1993). Thus, we tested whether the macroclimate may affect the regional waterbird pools in Europe, using five macroclimatic factors.

2. Material and methods

2.1. The species and the study area

We studied the distribution of 161 indigenous waterbirds inhabiting continental Europe, the British Isles and Iceland (see Appendix 1). It is difficult to make an exact delimitation of what is and what is not a waterbird. The Ramsar Convention calls waterbirds those birds that are ecologically dependent on wetlands. Its definition of wetlands includes marshes, fens, peatlands or water that is fresh, brackish or salt including coastal waters. The criterion used for this paper was to consider the species belonging to orders that are typically water-dependent. We included in the study the orders formed by the European swimming birds, diving birds, and wading birds. We also included the coastal distributions (< 1 km from the coast) of seabirds, because many species are frequently found in both marine and freshwater environments, and the inland dynamics of rivers affects production levels in coastal areas (Mann & Lazier 1991, Tucker & Evans 1997), so influencing the distributions of seabirds near the coast. Ospreys, marsh harriers, kingfishers, wagtails and warblers were not included because they belong to orders that are not ecologically dependent upon wetlands.

We used 55 river basins as OGUs (see Fig. 1 and Appendix 2) because the topography, the water availability and the evapotranspiration of river basins have great influence on the shape, length, caudal, seasonality, temperature and water composition of the fluvial net, which strongly affects the interchange of water, sediments, energy and nutrients among wetlands (Real et al. 1993, Tucker & Evans 1997). In addition, lower

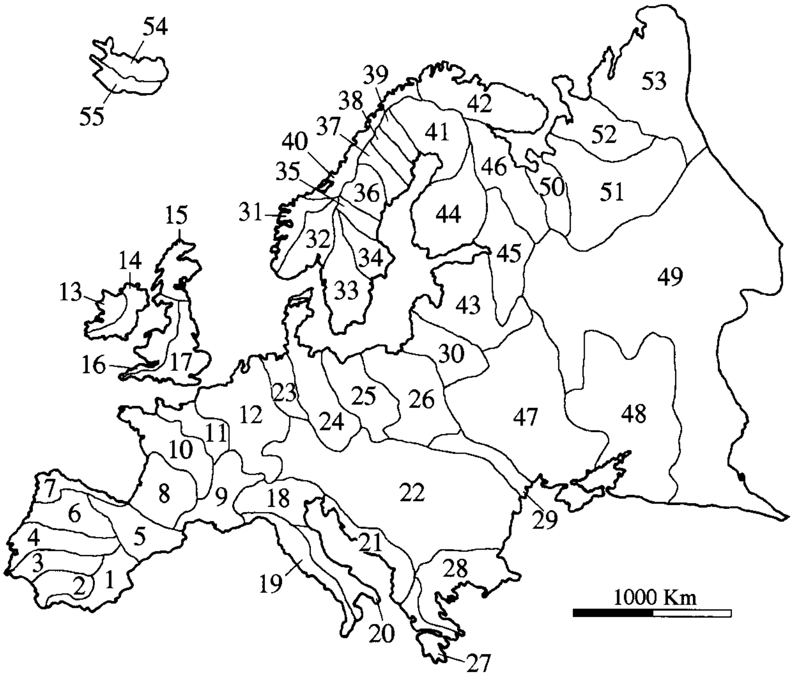

Fig. 1. European river basins considered in the analysis. The names of these basins are given in Appendix 2.

reaches of rivers carry high concentrations of oxygen, nitrates, phosphates, organic matter and suspended solids (Tucker & Evans 1997) that enrich coastal waters near the river mouths (Mann & Lazier 1991, Lalli & Parsons 1993), favouring the presence of birds throughout the coast (Hay 1992).

We joined together the contiguous small basins that flow into the same sea when elevation between them is low. The river basins north of the Black Sea and Caspian Sea are much larger than the other river basins in Europe. However, only the breeding species richness is correlated with the size of the basins ($r_{54} = 0.5479$, $p < 0.01$), whereas the species richness is unrelated to the size of the basins in the residence and wintering patterns.

Breeding areas (n = 149 species), wintering areas (n = 143 species), and residence areas (n = 95 species) were analyzed separately. We determined the presence of each waterbird species in each river basin from Cramp and Simmons (1977, 1980, 1983) and Cramp (1985) and completed the database using the following regional and local atlases: Sharrock (1976), Yeatman (1976), Rheinwald (1977), de Juana (1980), Shifferli et al. (1980), Muntaner et al. (1984), Álvarez et al. (1985), Elosegui (1985), Lack (1986), Devillers et al. (1988), Peris and Carnero (1988), Rufino (1990), Urios et al. (1991), Yeatman-Berthelot (1991), Brichetti et al. (1992), Ceballos and Guimerá (1992).

2.2. Classification analysis

We calculated the faunal similarities between each pair of basins using Baroni-Urbani and Buser's (1976) index

$$S = \frac{\sqrt{(CxD)} + C}{\sqrt{(CxD)} + A + B - C} \qquad (1)$$

where A is the number of species present in basin a, B is the number of species present in basin b, C is the number of species shared by the two basins, and D is the number of species absent from the two basins. This coefficient considers not only double presences but also double absences. In this way, shared absences increase the similarity between two basins when the absent species occur in other European basins, and so the similarities are considered in the context of the whole study area (Real et al. 1992c). The possibility of two basins being considered very similar only because of their shared absences is prevented by multiplying double absences by double presences.

Using the critical values in Baroni-Urbani and Buser (1976) we transformed the similarity matrix into a matrix of significant similarities, in which we replaced each value of the coefficient S by "+", "–" or "0", depending on whether the values of S were higher than, lower than, or similar to that expected at random, respectively (see Jackson et al. 1992, Real et al. 1992c, Márquez et al. 1997).

To group basins into biotic regions with similar waterbird fauna we used an agglomerative method of classification. Agglomerative techniques are preferred to divisive techniques because the former maximize the similarity within groups, which define biotic regions. Divisive techniques maximize the difference between groups, but do not guarantee within group similarity. We chose UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) because this is the agglomerative method that produces the least distortion in relation to the original distances between all pairs of samples (Sneath & Sokal 1973).

We represented the results as dendrograms. Starting from these dendrograms and the significant similarities, we modified the approach of McCoy et al. (1986) and Real et al. (1992b) for identifying significant biotic boundaries, either strong or weak, as follows.

Our null hypothesis was that biotic boundaries do not exist, but biotic spatial variation is gradual. Because of this, we started searching for boundaries on the level of the dendrogram with the lower similarity value, and from there we moved to the higher similarity nodes. This searching ended when no more significant boundaries appeared. This procedure does not contradict the use of an agglomerative classification, since biotic boundaries divide the space into biotic regions where the biotic affinity between OGUs is favoured by the agglomerative method.

For each dendrogram node we established a submatrix of significant similarities that only included the two groups of river basins separated by that one node, which we named group A and group B, respectively. This submatrix was divided into three zones: zone AxA and zone BxB, which corresponded to the significant similarities between OGUs of group A and between OGUs of group B, respectively; and zone AxB, corresponding to the significant similarities between the two groups of OGUs.

We call Pp(AxA) the number of pluses within zone AxA divided by the total number of pairwise basin comparisons in zone AxA. So, Pp(AxA) is the proportion of pluses in zone AxA. We call Psp(AxA) the number of basins in group A that have at least one plus divided by the total number of basins in group A. We can then compute d1(AxA) as follows: if the number of pluses in AxA is zero, then d1(AxA) = 0; otherwise,

$$\mathrm{d1(AxA)} = \frac{\mathrm{Pp(AxA)} \times \mathrm{Psp(AxA)}}{\sqrt{(\mathrm{Pp(AxA)})^2 + (\mathrm{Psp(AxA)})^2}} \quad (2)$$

The values of d1(AxA) range from 0 to 0.707, measuring the extent that similarities higher than expected at random (+) predominate within zone AxA.

We define Pm(AxA) and Psm(AxA) as the proportion of minuses in zone AxA and the proportion of basins in group A with at least one minus, respectively, and these are computed in the same way as Pp(AxA) and Psp(AxA), but taking into account the minuses. We then define d2(AxA) in the following way: if the number of minuses in zone AxA is zero, then d2(AxA) = 0; otherwise,

$$\mathrm{d2(AxA)} = \frac{\mathrm{Pm(AxA)} \times \mathrm{Psm(AxA)}}{\sqrt{(\mathrm{Pm(AxA)})^2 + (\mathrm{Psm(AxA)})^2}} \quad (3)$$

The values of d2(AxA) range from 0 to 0.707, measuring the extent that similarities lower than expected at random (–) predominate within zone AxA.

We define Pp(AxB) and Psp(AxB) in a similar way to Pp(AxA) and Psp(AxA), but with reference to zone AxB. So, d4 is zero when the number of pluses in AxB is zero; otherwise,

$$\mathrm{d4} = \frac{\mathrm{Pp(AxB)} \times \mathrm{Psp(AxB)}}{\sqrt{(\mathrm{Pp(AxB)})^2 + (\mathrm{Psp(AxB)})^2}} \quad (4)$$

The values of d4 range from 0 to 0.707, measuring the extent that similarities higher than expected at random (+) predominate within zone AxB.

The parameter DW(AxA) measures to what extent the similarities that are higher than expected (+) are in zones AxA but not in AxB (see McCoy et al. 1986), where DW(AxA) = d1(AxA) – d2(AxA) – d4.

Similarly, DW(BxB) = d1(BxB) – d2(BxB) – d4, where d1(BxB) and d2(BxB) are calculated as d1(AxA) and d2(AxA), but computing the pluses and minuses in zone BxB. The average of DW(AxA) and DW(BxB), named DW, measures to what extent similarities that are higher than expected (+) are in either zones AxA or BxB but not in AxB.

We define d3 in the same way as d4, but computing the minuses in AxB. We then compute the parameter DS = d3 – d4 – (22(AxA) + d2(BxB))/2, which gives a measure of whether the similarities that are lower than expected (–) are located in AxB, but not in AxA or BxB.

The statistical significance of a node was assessed using a G-test of independence (Sokal & Rohlf 1981, McCoy et al. 1986) of the distribution of the signs "+", "–" and "0" in the three zones of the submatrix, and so we obtained the parameters GW, for weak boundaries, and GS, for strong boundaries. If similarities higher than expected (+) are significantly located in zones AxA or BxB, but not in AxB, that is, if $DW > 0$ and GW is significant, then there is at least a weak biotic boundary between both groups of basins. In this case, if $DW(AxA) > 0$ then the group of basins A constitutes a biotic region, and the same applies for DW(BxB) and the group of basins B. If similarities lower than expected (–) are significantly located in AxB, but not in AxA or BxB, that is, if $DS > 0$ and GS is significant, then a strong biotic boundary exists between the groups of basins. The areas delimited by strong boundaries are biotic supraregions. A supraregion can contain several biotic regions separated by weak boundaries.

We obtained trees of OBUs by representing only the nodes that corresponded to biotic boundaries.

We considered each biotic boundary as either impermeable, semipermeable, or permeable. A boundary is impermeable if groups of basins A and B share no species. The boundary is semipermeable if all species present on one side are also present on the other side, but not vice versa. A boundary is permeable if some species present in A are absent from B, and vice versa.

A permeable boundary can be balanced or unbalanced. If the number of species present in A is the same as the number of species present in B, then the boundary is balanced, else it is unbalanced.

There is no species replacement through a semipermeable boundary, but the species number at both sides of the boundary varies. If a permeable boundary is balanced, a species replacement occurs through the boundary, but not a change in species number. If a boundary is unbalanced, both a species replacement and a variation of species number occur through the boundary.

2.3. Climatic characterization of the biogeographical patterns

We characterized the biogeographical patterns according to five environmental factors using the variables in Table 1:

— Annual climatic stability: some species could

Table 1. Variables used in the analysis.

Environmental factor	Variable	Code
Annual climatic stability	Annual temperature range[1]	(TR)
Availability of water	Mean annual precipitation[1]	(P)
Availability of energy	Mean annual temperature[1]	(T)
	Mean temperature of January[1]	(JanT)
	Mean temperature of July[1]	(JulT)
	Potential evapotranspiration[2]	(PET)
Simultaneous availability of water and energy	Actual evapotranspiration[2]	(AET)
Surface	Area of the river basin[3]	(A)
	Absolute potential evapotransp.[4]	(APET)
	Absolute actual evapotransp.[4]	(AAET)

Sources: [1]World Meteorological Organization (1970); [2]USSR National Committee for the International Hydrological Decade (1977); [3]The Times atlas of the world (1988); [4]APET = A * PET, AAET = A * AET.

not be resident if their physiology does not tolerate a great intraannual environmental variation.

- Availability of water: water is sometimes considered important to account for bird distributions (e.g. Crowe & Crowe 1982), specially if birds are linked to water-related ecosystems. In addition, the run-off of rivers in the sea may affect coastal productivity (Mann & Lazier 1991, Lalli & Parsons 1993).
- Availability of energy: some species may not satisfy their physiological needs, and so reduce their competitive capacity, if the availability of energy is low (Hutchinson 1959, Brown 1981, Wright 1983); on the other hand, a warm climate may cause physiological stress to some species (Koskimies & Lahti 1964).
- Simultaneous availability of water and energy: this factor may control the productivity of river basins (Major 1963, Rosenzweigh 1968), thus affecting the species composition of each basin.
- Surface: the area of a river basin may affect its species composition by stochastically increasing the number of species (Preston 1962), or by increasing the whole amount of water and energy that is collected by the basin (Wright 1983).

Annual temperature range (TR) was used for characterizing only the residence boundaries, whereas mean temperature of January (JanT) was used for the wintering and residence boundaries, and mean temperature of July (JulT) was used for the breeding and residence boundaries. We used JanT and JulT because they refer to the coldest and the warmest month, respectively. We used the area of the river basins (A) to test the stochastic influence of the OGU's size on the faunal composition, and the absolute evapotranspirations (APET = A * PET, and AAET = A * AET) to test the influence of the OGU's size due to the whole amount of energy, or energy plus water, seized by the basins. Higher APET or AAET could cause a higher net transport of nutrients from the mountains to the valleys within the basin (Tucker & Evans 1997), and to the coastal waters off the mouth of the rivers (Lalli & Parsons 1993).

We used multiple stepwise logistic regression to characterize the biotic boundaries, using the variables shown in Table 1. The goodness of fit was evaluated by means of a χ^2 test, and the estimation of the parameters in the logistic function was by maximum likelihood and tested using Wald's (1943) test. We only accepted a model if at least 60% of the basins on each side of the boundary were correctly predicted by the model.

We used Canonical Variate Analysis (CVA) (ter Braak 1988) to order the biotic regions along the main climatic gradients defined via Canonical Correspondence Analysis (CCA) (Chessel et al. 1987). We positioned the biotic regions along axes representing the main macroclimatic gradients related to their basins. We used the fraction of the total variance in the climatic data extracted by each axis (FR-extracted) to select those axes most related to the climate.

3. Results

3.1. Breeding boundaries and regions

The regionalization for breeding waterbirds yields two breeding biotic supraregions, subdivided into a total of six biotic regions (see Fig. 2 and Table 2). The biotic supraregions follow a latitudinal pattern, whereas the biotic regions follow a mainly longitudinal pattern. The Northern Breeding Supraregion (NBS) is smaller, contains less biotic regions and is poorer in species than the Southern Breeding Supraregion (SBS) (Fig. 2). The boundary between Biotic Region B6 and the rest of the SBS is semipermeable because all species breeding in B6 also breed in either B3, B4 or B5 (Fig. 2c). The boundaries between B1 and B2, and between B4 and B5 are unbalanced because there are many more species breeding in B1 but not in B2 than vice versa (Fig. 2c), and there are many more species breeding in B4 but not in B5 than vice versa (Fig. 2c).

Only three biotic boundaries are well characterized by logistic regressions (Fig. 2c). Though the breeding species richness is correlated with the size of the basins ($r_{54} = 0.5479$, $p < 0.01$), differences in the surface of the basins, related to potential evapotranspiration, only characterizes the biotic boundary between regions B4 and B5 (Fig. 2c, Table 1). The strong boundary and the boundary between B3 and B4–B5 are characterized by differences in the availability of energy (Fig. 2c; Table 1).

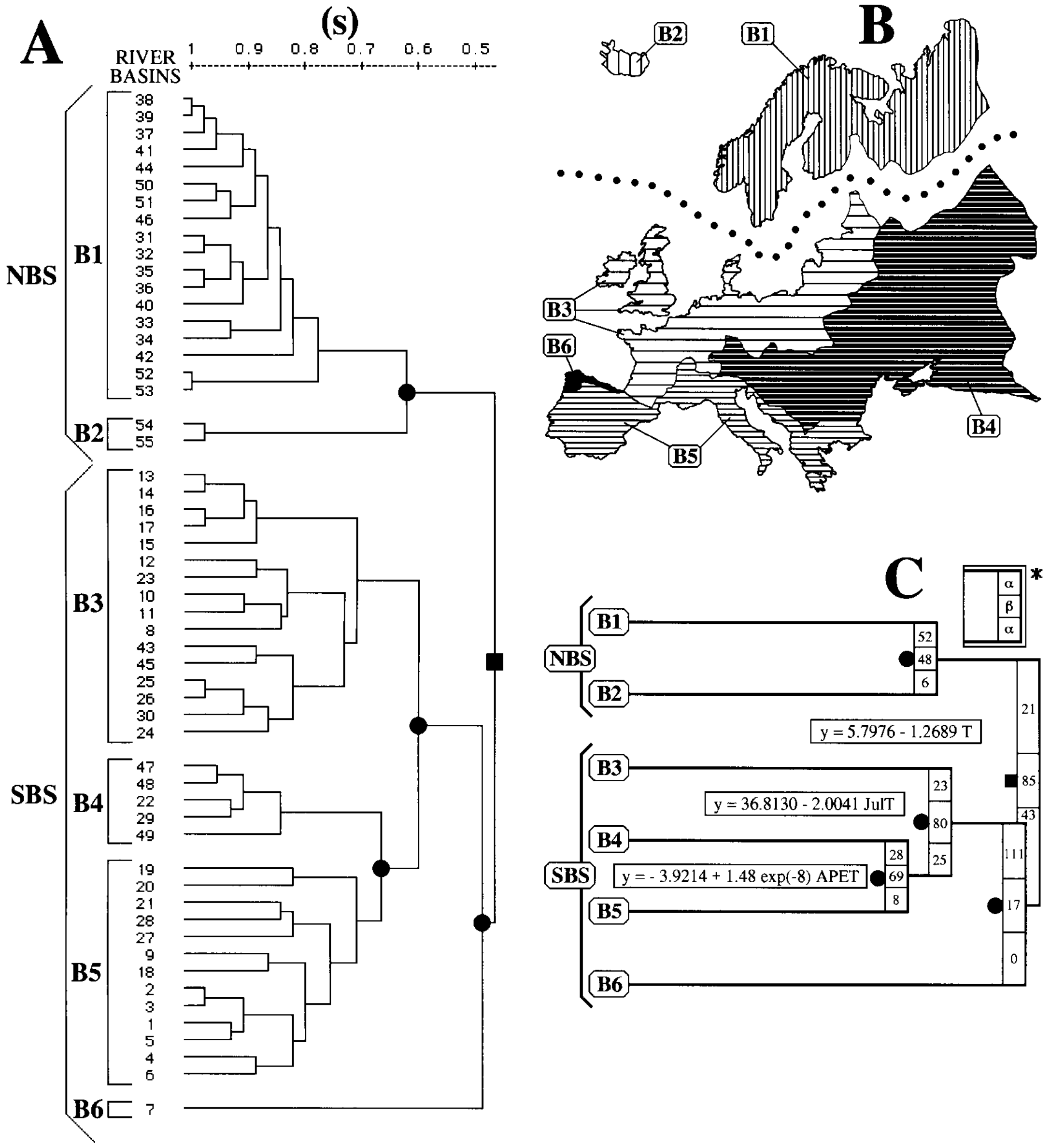

Fig. 2. Breeding biotic regions for waterbirds in Europe. (2a) Dendrogram based on the Baroni-Urbani & Buser's similarity index (S). Black squares: strong boundaries; black circles: weak boundaries; NBS: Northern Breeding Supraregion; SBS: Southern Breeding Supraregion. (2b) Map of biotic regions and boundaries. Dot lines: strong boundary. (2c) Tree of OBUs. y: logit functions for the boundaries with significant logistic regression. *: α = species number on just one side of the boundary; β = species number on both sides of the boundary. Codes of variables as in Table 1.

CVA axes I and III show the highest FR-extracted (Table 3). The sum of all the canonical eigenvalues represents 51.02% of the inertia (= sum of all unconstrained eigenvalues). This implies that 51.02% of the variation existing within the set of regions can be explained by the CVA with the variables used. Axis I represents the main environmental gradient affecting breeding waterbird species composition of the basins. This is a gradient of environmental energy, because it is mainly correlated with the three variables related to this climatic factor (PET, T, and JulT) (Table 3; Fig. 3), and is highly correlated with geographical latitude ($r_{54} = -0.9606$, $p < 0.01$). Axis III is a secondary environmental gradient mostly correlated with the absolute potential evapotranspiration (APET) (Table 3; Fig. 3). This is a gradient of surface of the basins, but referred to the energy seized by the whole area of the basins, as opposed to the energy available per surface unit, and is correlated with geographical longitude ($r_{54} = 0.7430$, $p < 0.01$).

3.2. Wintering boundaries and regions

The regionalization for wintering waterbirds shows two wintering biotic supraregions, with three wintering biotic regions each (see Fig. 4 and Table 2). The strong boundary between both wintering supraregions is more southern in intermediate longitudes than the breeding strong boundary. The Northern Wintering Supraregion (NWS) is smaller and is remarkably poorer in species than the Southern Wintering Supraregion (SWS) (Fig. 4). The boundary between Biotic Region W3 and the rest of the NWS is semipermeable because all species wintering in either W1 or W2 also winter in W3, but not vice versa (Fig. 4c). The number of waterbird species increases from the eastern region W1 (with 27 species) to the central region W2 (with 37 species) and to the western region W3 (with 72 species) (see Appendix 1). The boundary between W4 and the rest of the SWS is very unbalanced because there are many more species wintering in either W5 or W6 but not in W4 than vice versa (Fig. 4c).

Four of the five biotic boundaries are well char-

Table 2. Significant boundaries between the river basins on the dendrogram's forks. DW > 0 and significant GW indicate a weak boundary between the groups; DS > 0 and significant GS indicate a strong boundary between the groups. NS = p ≥ 0.01; * = p < 0.01; ** = p < 0.005.

Groups set up by UPGMA		Boundaries					
Group A	Group B	Weak			Strong		
		DW	GW	p	DS	GS	p
BREEDING							
B4	B5	0.4391	21.1806	**	– 0.5361	0.0000	NS
B1	B2	0.4657	39.8054	**	– 0.4828	0.0000	NS
B3	B4 + B5	0.4603	137.5494	**	– 0.4429	1.3393	NS
B3 + B4 + B5	B6	0.2341	44.4427	**	– 0.0436	6.5931	NS
B1 + B2	B3 + B4 + B5 + B6	0.5061	385.9572	**	0.0848	375.0311	**
WINTERING							
W1	W2	0.4036	13.9863	**	– 0.6032	0.0000	NS
W5	W6	0.3811	24.6834	**	– 0.6482	0.0000	NS
W4	W5 + W6	0.5724	169.2981	**	– 0.2394	0.0000	NS
W1 + W2	W3	0.5432	141.3324	**	– 0.2665	0.0082	NS
W1 + W2 + W3	W4 + W5 + W6	0.5325	692.5558	**	0.4226	769.5467	**
RESIDENCE							
R1	R2	0.3982	8.2106	**	– 0.6178	0.0000	NS
R4	R5	0.4449	14.2989	**	– 0.5039	0.0000	NS
R3	R4 + R5	0.5969	59.1566	**	– 0.1294	0.0000	NS
R1 + R2	R3 + R4 + R5	0.5103	144.0668	**	– 0.0975	3.5594	NS
R1 + R2 + R3 + R4 + R5	NWRS	0.3333	147.5925	**	0.1576	157.4342	**
NBRS	NERS	0.5215	7.7905	*	0.0605	8.6191	**
R1 + R2 + R3 + R4 + R5 + NWRS	NBRS + NERS	0.2248	94.0119	**	0.2376	446.2259	**

acterized by logistic regressions (Fig. 4c). The strong boundary is well characterized by differences in availability of energy, and secondarily by differences in size of the basins (Fig. 4c, Table 1), that is to say, the basins of the NWS are colder, and when a basin of the SWS is also cold it is larger than the basins of the NWS. The boundary between W1 and W2, and the boundary between W5 and W6 are only characterized by differences in the availability of energy (Fig. 4c, Table 1). The boundary between W3 and W1–W2 is characterized by differences in availability of water (Fig. 4c, Table 1).

CVA axes I and II show the highest FR-extracted (Table 3). The sum of all the canonical eigenvalues represents 45.66% of the total inertia. Axis I represents a gradient of environmental energy, because it is mainly correlated with the three variables related to this climatic factor (T, PET and JanT) (Table 3; Fig. 5), and is correlated with both geographical latitude ($r_{54} = 0.9420$, $p < 0.01$) and longitude ($r_{54} = 0.5350$, $p < 0.01$). Axis II is mostly correlated with mean annual precipitation (P) (Table 3; Fig. 5), and so it is a gradient of water availability, and is correlated with geographical longitude ($r_{54} = 0.5988$, $p < 0.01$).

Table 3. CVA of breeding, wintering and resident biotic regions. Eigenvalues and fraction of variance in environmental data (FR) extracted by the first four axes. Intraset correlations between the two axes with highest FR-extracted and the climatic variables. Codes of variables as in Table 1.

	1	2	3	4
Breeding axes:				
Eigenvalue	0.897	0.717	0.519	0.392
FR-extracted	0.498	0.066	0.072	0.055
Intraset correlation — Breeding axes:				
P	- 0.001		- 0.326	
T	0.939		- 0.288	
JulT	0.926		0.149	
PET	0.946		0.040	
AET	0.780		- 0.318	
APET	0.302		0.719	
Wintering axes:				
Eigenvalue	0.907	0.704	0.419	0.242
FR-extracted	0.491	0.071	0.067	0.027
Intraset correlation — Wintering axes:				
P	- 0.275	0.441		
T	- 0.972	0.108		
JanT	- 0.882	0.380		
PET	- 0.923	- 0.286		
AET	- 0.742	0.243		
APET	- 0.214	- 0.332		
Residence axes:				
Eigenvalue	0.922	0.797	0.524	0.361
FR-extracted	0.467	0.093	0.088	0.019
Intraset correlation — Resident axes:				
P	- 0.250	0.397		
T	- 0.980	0.018		
TR	0.593	- 0.599		
JulT	- 0.742	- 0.408		
JanT	- 0.918	0.256		
PET	- 0.900	- 0.393		
AET	- 0.686	0.160		
AAET	- 0.007	- 0.066		

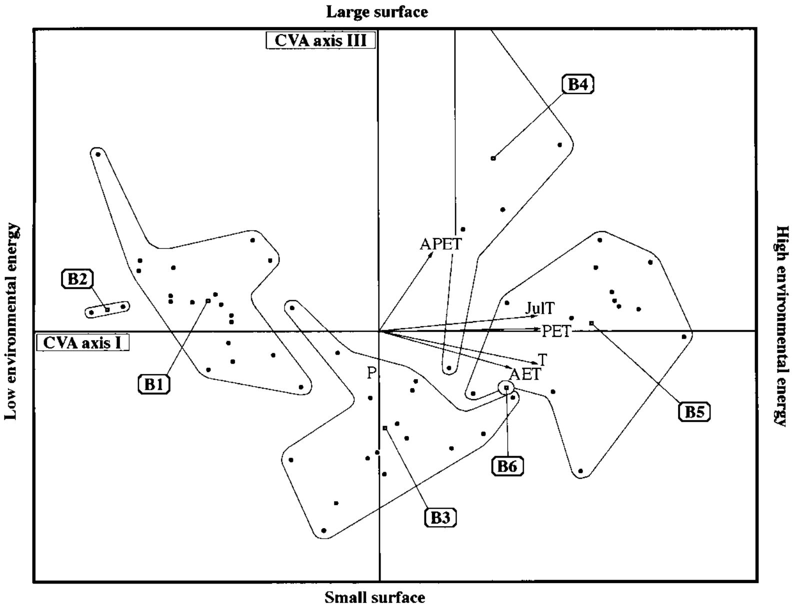

Fig. 3. CVA analysis of the breeding biotic regions. Biplot of climatic variables (arrows) and biotic regions on axes I and III. Dots represent the river basins. Squares represent the centroids of the basins for each biotic region. Basins in the same biotic region are rounded together by a line. Codes of variables as in Table 1.

3.3. Residence boundaries and regions

The regionalization for resident waterbirds is more fragmented than those obtained for either breeding or wintering waterbirds. There are four biotic residence supraregions, one of them, the Southern Residence Supraregion (SRS), subdivided into five biotic regions (see Fig. 6 and Table 2). The Onega, Northern Dvina and Mezen basins were not classified because they harbour no resident waterbirds. The three strong boundaries are either semipermeable or very unbalanced (Fig. 6c), and so the number of species decreases from the Southern Residence Supraregion (SRS) to the North-Western Residence Supraregion (NWRS), and from here to the North-Baltic Residence Supraregion (NBRS) and even more to the North-Eastern Residence Supraregion (NERS) (Fig. 6c). In the SRS, only the boundary between R3 and R4–R5 is markedly unbalanced (Fig. 6c).

Two strong boundaries and three weak boundaries are significantly characterized by logistic regressions (Fig. 6c). Two strong biotic boundaries and two weak boundaries are characterized by differences in the availability of energy (Fig. 6c; Table 1). In the strong boundary between the SRS and the NWRS, the surface of the basins (A) complements the mean annual temperature (T), though T itself can generate a significant model and predict correctly more than 84.6% of the basins on each side of the boundary. The boundary between R3 and R4–R5 is characterized by differences in the surface of the basins, related to potential evapotranspiration (Fig. 6c; Table 1).

CVA axes I and II show the highest FR-extracted (Table 3). The sum of all the canonical eigenvalues represents only 38.21% of the total inertia. Axis I, as for breeding and wintering waterbirds, is a gradient of environmental energy, because it is mainly correlated with the four variables related to this climatic factor (T, JanT, PET, and JulT) (Table 3; Fig. 7), and is correlated with geographical latitude ($r_{51} = 0.9461$, $p < 0.01$) and longitude ($r_{51} = 0.4837$, $p < 0.01$). Axis II is mostly correlated to annual temperature range (TR) (Table 3; Fig. 7). This is a gradient of climatic stability, and is correlated with geographical longitude ($r_{51} = -0.4864$, $p < 0.01$).

4. Discussion

4.1. Comparison between breeding, wintering, and residence patterns

We detected a discrete pattern of geographical change in the species pools of the European basins for the breeding, wintering, and resident waterbirds.

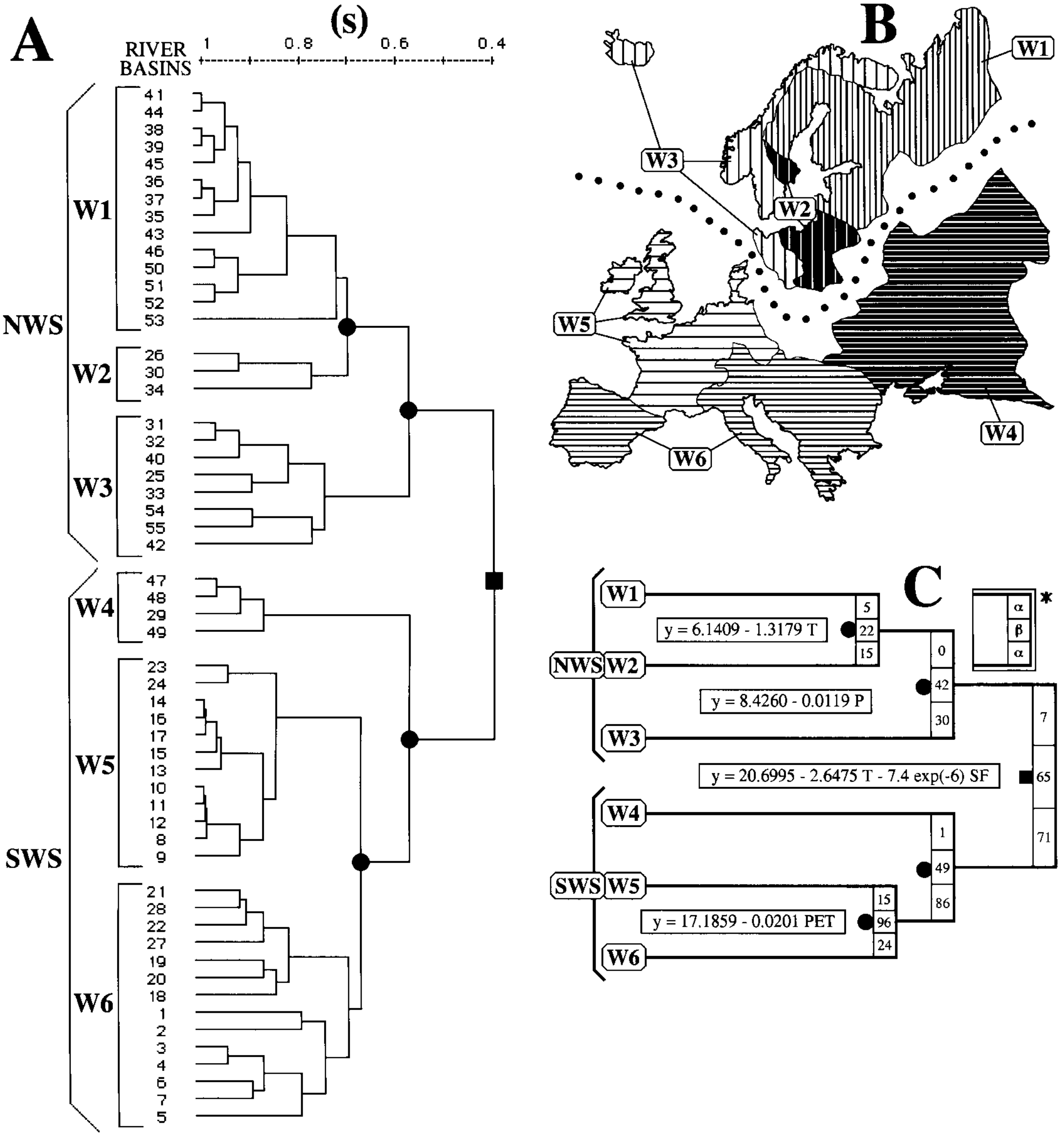

Fig. 4. Wintering biotic regions for waterbirds in Europe. (4a) Dendrogram based on the Baroni-Urbani & Buser's similarity index (S). Black squares: strong boundaries; black circles: weak boundaries; NWS: Northern Wintering Supraregion; SWS: Southern Wintering Supraregion. (4b) Map of biotic regions and boundaries. Dot lines: strong boundary. (4c) Tree of OBUs. y: logit functions for the boundaries with significant logistic regression. *: α = species number on just one side of the boundary; β = species number on both sides of the boundary. Codes of variables as in Table 1.

In the breeding and wintering seasons we detected a similar latitudinal pattern for the strong boundaries and an overall longitudinal pattern for the weak boundaries.

Inside the northern supraregions, the wintering region W3 includes the north-western continental coast of Europe and Iceland (Fig. 4b). However, during the breeding season, Iceland (B2) is biotically differentiated from northern continental Europe (B1) (Fig. 2b; Appendix 1). The cause of this is not a spatial breeding segregation of the species wintering in the north, since only 4 of the

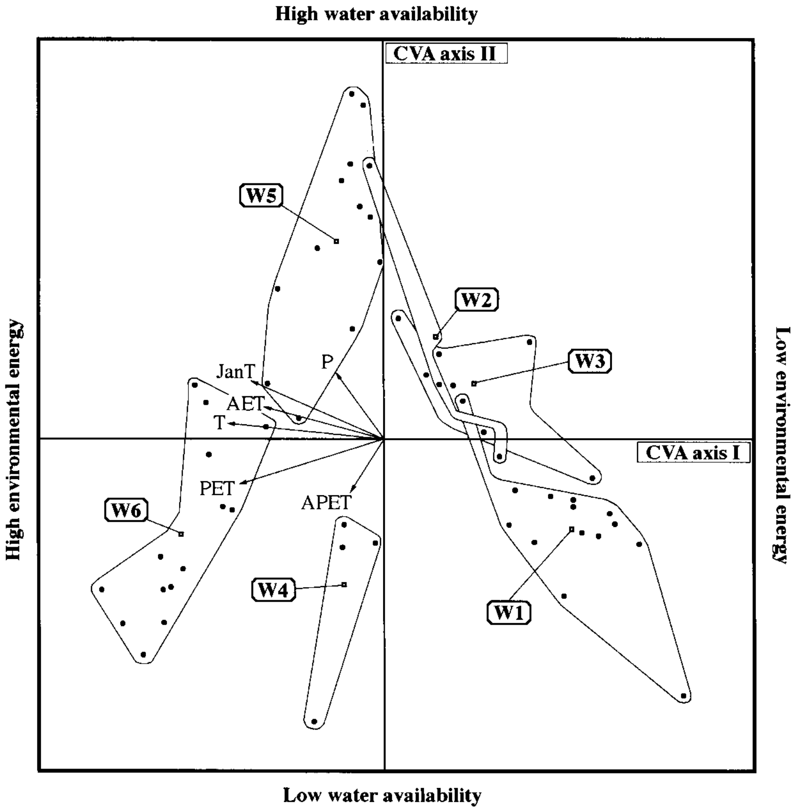

Fig. 5. CVA analysis of the wintering biotic regions. Biplot of climatic variables (arrows) and biotic regions on axes I and II. Dots represent the river basins. Squares represent the centroids of the basins for each biotic region. Basins in the same biotic region are rounded together by a line. Codes of variables as in Table 1.

41 waterbirds wintering in both Iceland and the continental coast breed in just one of them. The differentiation is due instead to the 42 migrant birds coming from the south of Europe to breed in the North of Europe, since 29 of them breed only in the northern continental basins and 2 of them breed exclusively in Iceland.

Inside the southern supraregions, both SBS and SWS contain a Mediterranean region (B5 and W6), an Atlantic region (B3 and W5), and a South-Eastern region (B4 and W4). However, the hierarchical relation between these regions is different in each case: the Mediterranean region is biotically closer to the South-Eastern region in the breeding season (Fig. 2a), but to the Atlantic region in winter (Fig. 4a). This is because most species that breed exclusively in both the Mediterranean and South-Eastern regions (B4 and B5) winter in the Mediterranean region but not in the South-Eastern one, while most species breeding only in the Atlantic region (B3) winter in both the Mediterranean and Atlantic regions but not in the South-Eastern one. The Danube river has a pivotal role between the Mediterranean and South-Eastern Regions, because it belongs to the South-Eastern Region in the breeding season but to the Mediterranean Region during the wintering season.

The residence pattern is more fragmented than the wintering and breeding patterns. This fact seems consistent with the predictions of Järvinen and Väisänen (1980) that sedentary bird species are expected to have more pronounced between-zone differences than migrant birds. They suggest that more mobility leads to more 'fine-grained' use of habitat, which might make migrant species less dependent on specific conditions than resident species. Guillet and Crowe (1985) also considered that the less fragmented regionalization of Africa based on waterbird distributions, compared with the regionalization based on all bird distributions (Crowe & Crowe 1982), is mainly due to the higher mobility of waterbirds.

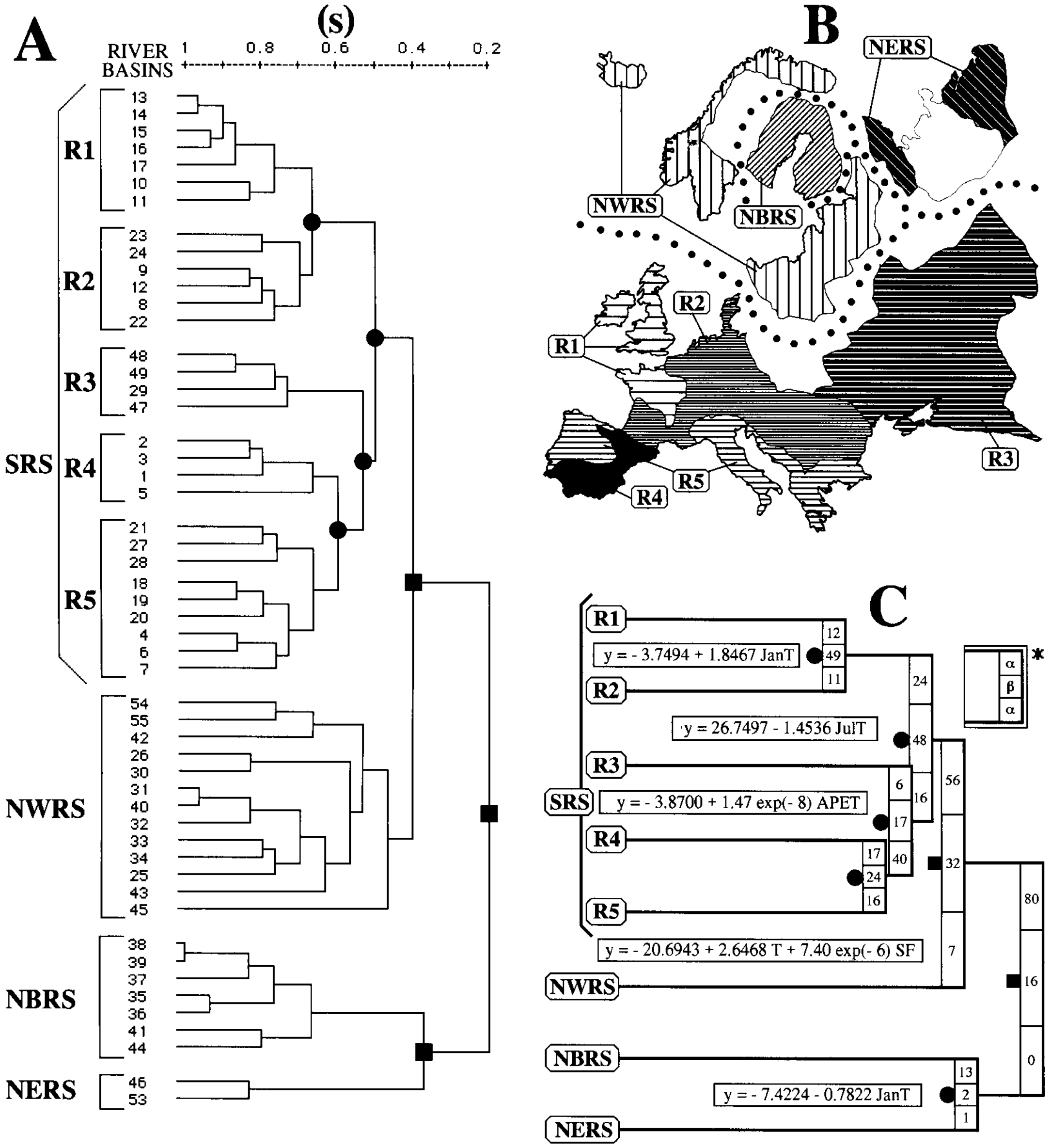

Fig. 6. Resident biotic regions for waterbirds in Europe. (6a) Dendrogram based on the Baroni-Urbani & Buser's similarity index (S). Black squares: strong boundaries; black circles: weak boundaries; NWRS: North-Western Residence Supraregion; NBRS: North-Baltic Residence Supraregion; NERS: North-Eastern Residence Supraregion; SRS: Southern Residence Supraregion. (6b) Map of biotic regions and boundaries. Dot lines: strong boundary. (6c) Tree of OBUs. y: logit functions for the boundaries with significant logistic regression. *: α = species number on just one side of the boundary; β = species number on both sides of the boundary. Codes of variables as in Table 1.

4.2. The role of environmental energy

In our study, the variables related to environmental energy, or area related to energy, characterized 11 of the 12 climatically explained boundaries. In the characterization of the biotic regions by CVA, available energy was always the most important factor. This coincides with Harrison

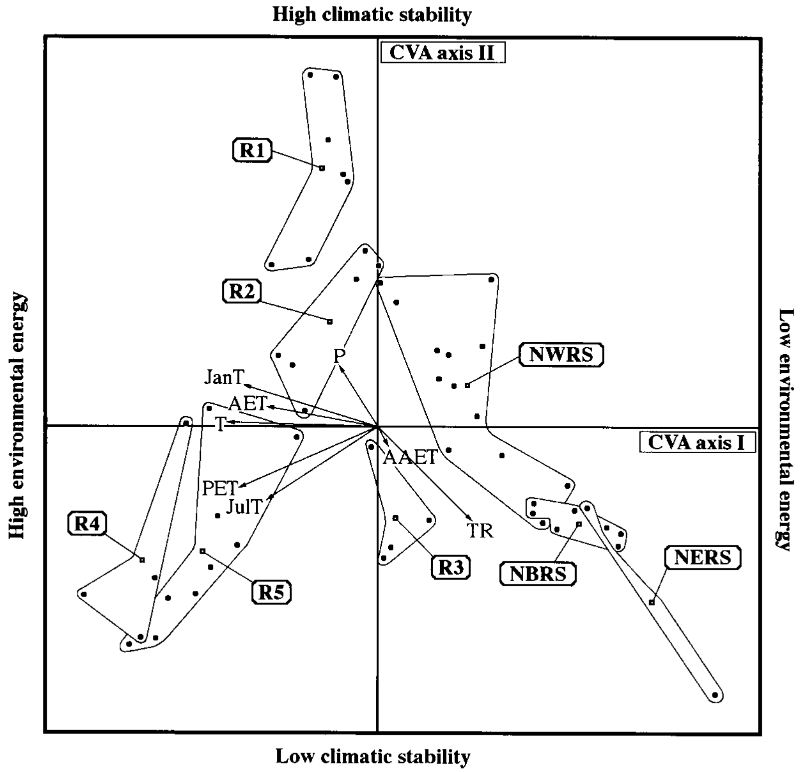

Fig. 7. CVA analysis of the resident biotic regions. Biplot of climatic variables (arrows) and biotic regions on axes I and II. Dots represent the river basins. Squares represent the centroids of the basins for each biotic region. Basins in the same biotic region are rounded together by a line. Abbreviated supraregion names as in Fig. 6. Codes of macroclimatic variables as in Table 1.

(1982), who considered that temperature is the more obvious factor governing the distribution of birds.

Environmental energy may affect species composition of the basins in several ways. Hutchinson (1959) proposed that energy may determine species richness, because a population needs a minimum amount of environmental energy to survive (see also Brown 1981, Wright 1983). This hypothesis was found consistent with data in some studies about birds (Rabinovich & Rapoport 1975, Turner et al. 1988), and might explain the decrease of waterbird species in the Northern Supraregions in relation to the Southern Supraregions.

Turner et al. (1988) considered that available energy might explain the species richness of insectivorous birds in Great Britain indirectly, through overall productivity. However, productivity depends not only on the environmental energy, but also on the water available. Major (1963) and Rosenzweig (1968) recommended the use of precipitation (P) and actual evapotranspiration (AET) as indicators of productivity. We found these variables less explanatory than the variables that refer to environmental energy but not to productivity (T, JanT, JulT and PET). This result suggests that the effect of energy availability on waterbirds on a continental scale is unrelated to productivity.

The energy theory also predicts that the warm season will support more species than the cold season, but this is only true in the Northern Supraregion, whereas the Southern Supraregion supports more species in the wintering season than in the breeding season (136 vs. 128 species). Besides, the Southern Supraregions in the breeding pattern and in the residence pattern also contradict the energy theory, because in both cases the biotic region with lower JulT supports more species than the regions with higher JulT (see Figs. 2c and 6c, and Appendix 1). These results suggest the existence of a heat stress affecting waterbirds during summer in the Southern Supraregions. Koskimies and Lahti (1964) and Beintema and Visser (1989) postulated that the high energy level during the breeding season in the southern areas would cause an environmental stress on the species with a thermoregulation system that develops earlier. An earlier development of thermoregulation allows chicks to be more resistant to cold temperatures, but implies a higher energy intake and a high metabolic rate that can cause problems in warm weather, and even put a southern limit to the distribution of species in Europe (Koskimies & Lahti 1964). In this way, Beintema and Visser (1989) considered that this is the reason for the greater limitations on the Scolopacidae being able to live in the south in comparison with the Charadriidae. The Charadriidae have poorer thermoregulation, longer dependence on brooding, slower development, and longer life spans when compared with the Scolopacidae (Beintema & Visser 1989). Our results agree with these authors, because 88.9% of the European Charadriidae species occur in the SBS and only 66.7% occur in the NBS, whereas 95.8% of the Scolopacidae species occur in the NBS and only 79.2% occur in the SBS. In B5, the warmest region of Europe, only 25% of the European Scolopacidae species breed, whereas 44% of the Charadriidae species breed there.

4.3. The role of precipitation

Precipitation was a secondary factor in the characterization of the wintering biotic regions by CVA. Only the semipermeable boundary that separates W3 from W1 and W2 (Fig. 4c) was characterized by differences in precipitation. Most waterbirds in these regions winter exclusively out to sea, but inland precipitation seems to determine their wintering coastal distribution. Precipitation has a great influence on the amount of water flowing in the rivers, and thus on the feeding conditions for seabirds near the coast. According to Mann and Lazier (1991), rivers entering the sea often carry high nutrients that enrich coastal waters and increase productivity off the mouth of the rivers. Besides, the flow of the rivers at the sea surface causes nutrients to be entrained from deeper waters that are rich in phosphates and nitrates (upwelling), thus contributing to phytoplankton blooms off the river mouth (Lalli & Parsons 1993).

Rainfall is considered the main factor characterizing the geographical classification for birds in Africa (Crowe & Crowe 1982, Guillet & Crowe 1985, 1986), and in the northern territory of Australia (Whitehead et al. 1992), although in Europe no inland distribution pattern for waterbirds was characterized by precipitation. Europe has relatively more precipitation and less evapotranspiration than all other continents (Hammer 1986), and semiarid climates in Europe are restricted to some southern areas. Wetlands exist even in the most arid regions, and they are widely inhabited by waterbirds. So, aridity is not a strong gradient in Europe that could cause great faunal differences between areas, as occurs in Africa or in Australia.

4.4. Comparison with biogeographical patterns of other organisms

The comparison of these pattern with other well-studied groups could suggest a linkage between the processes that produce them (Sætersdal & Birks 1993, Mönkkönen & Viro 1997).

The Northern Supraregions contain the Arctic tundra and the boreal coniferous forest, whereas the temperate forest, the temperate grassland, and Mediterranean vegetation are included in the Southern Supraregions. The basins characterized by mixed forest, situated between the boreal coniferous forest and the temperate forest, are included in the Southern Supraregion during the breeding season, but are included in the Northern Supraregions in the wintering and resident patterns.

The European biogeographical patterns previously obtained using snakes and lizards (Ramírez et al. 1992), amphibians (Real et al. 1992a), and mammals (Grabinska 1994) also yielded a northern large region characterized by a lower number of species than a southern region. However, there are two main differences between the patterns obtained for these terrestrial vertebrates and the patterns for waterbirds: (1) For terrestrial vertebrates the Iberian Peninsula is always separated from the other Mediterranean peninsulas by a biotic boundary. During the glaciations, the three Mediterranean Peninsulas became isolated refuges for the terrestrial populations, favouring the differentiation of a characteristic fauna in each peninsula (Harrison 1982). After the glaciations this biogeographical pattern in the terrestrial fauna can still be observed, possibly due to the limited power of dispersion of these species (Real et al. 1992a). The Iberian Peninsula is the most distant peninsula, and the Pyrenees function as an effective barrier to terrestrial organisms. However, the avifauna have a higher capacity of dispersal which may have allowed them to move from one peninsula to the others, and quickly reach the rest of the continent after the glaciations, constituting biotic regions more related to climate than to historic events. (2) The British Isles are associated with the northern areas of continental Europe for terrestrials vertebrates whereas for waterbirds they are associated with the Southern Supraregions. The number of species of these terrestrial vertebrates decreases in the north of Europe because of its harsher climate, and also in the British Isles because of their insularity, joining both areas together in a region with low species richness. However, insularity is not relevant for airborne species such as waterbirds and so the British Isles are associated with the climatically similar central Europe.

Our biogeographical regionalizations for waterbirds are less fragmented than those of more sedentary organisms, such as limnofauna (Illies 1978), *Salix* species (Myklestad & Birks 1993) and pteridophytes (Birks 1976). This is consistent with the results obtained by Sætersdal and Birks (1993), who noted that birds generate a surprisingly homogeneous pattern in contrast to plants, which they attributed to the higher mobility of birds.

4.5. Biotic Regions and Conservation

The contribution of this biotic regionalization to conservation policy is the establishment of a context for decision-making in Europe on the continental scale, in terms of biogeographical representativeness for waterbirds. The regionalization by means of land classification has been defined as the central problem to implementing the idea of representativeness (Austin & Margules 1986, Sætersdal & Birks 1993). This concept is a criterion for the conservation of species and communities that aims to ensure that the whole range of biotic variation is contained in the designed reserve system. In this framework, biotic regions are areas with characteristic combinations of species that can be used to evaluate the biogeographic representativeness of the reserve system (Austin & Margules 1986). Once the study area has been regionalized, the representativeness of a reserve indicates the degree to which this reserve supports most of the species of the biotic region where it is located; the representativeness of the reserve system indicates the degree to which the species of all biotic regions are contained in the set of reserves. According to this, different evaluation criteria, such as species richness, rarity, naturalness, or complementarity (Margules 1986, Ramírez & Vargas 1992, Williams et al. 1996), are to be used to decide which areas inside each biotic region are best for conservation, when compared with the other reserves that belong to the same biotic region. This evaluation must be repeated independently inside each biotic region, to ensure the final representativeness of the reserve system in the whole study area.

Our results also highlight the need of different frameworks for conservation depending on whether breeding, wintering or resident waterbird populations are the object of protection. Both breeding and wintering seasons are important for the success of waterbirds throughout their biological cycle. Because of this, the representativeness for waterbirds must observe the existence of different biogeographical patterns in each season, which are the result of a strong spatial reorganization of populations during the year.

River basins are in many cases managed as geographical administrative units, despite being often cut by political frontiers. Owing to the dynamics of water flows, a basin scale has been considered necessary for any conservation programme designed for wetlands in Europe (Tucker & Evans 1997). This makes river basins suitable OGUs when the results of classification are to be used in conservation policy. The value for conservation of each river basin must be sought in further investigations. The selection of more specific sites, as particular reserves, should require a more local and ecological approach.

The macroclimatic characterization of the biotic regionalizations also provides some considerations related to conservation. Among the factors considered for the characterization, water availability is the only one that can be directly influenced by human activities. Storing water inside the river basins at times of high flow, and releasing water during times of low natural river flow, has the effect of modifying the seasonal pattern of river run-off to which the organisms have become adapted over long periods of time (Mann & Lazier 1991). However, only one northern wintering boundary is characterized by differences in water availability, and paradoxically most species affected by this boundary are marine. This suggests that management of river basins may condition the maintenance of northern coastal regionalizations only. The most important factor that explains the regionalization of Europe for waterbirds is the energy availability, which is not directly affected by human activity. So, human uses of basins may have a low effect on the regionalization patterns described here, except those effects related with a possible climate change due to the greenhouse effect. This is not to say that human activities do not affect local environments and wetlands, but that the overall regionalization pattern in Europe depends on a natural process that is not related to human activities, and thus must be taken into account when designing the reserve framework in Europe.

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Selostus: **Vesilintujen levinneisyys Euroopassa: eläinmaantieteellinen aluejako ja suurilmasto**

Kirjoittajat tutkivat pesivien ja talvehtien vesilintujen (mukaanlukien kaikki vesiympäristön lajit, ks. Liite 1) levinneisyyden säännönmukaisuuksia Euroopassa. Erityisenä tavoitteena oli selvittää ovatko muutokset vesilinnuston rakenteessa alueelta toiselle siirryttäessä vähittäisiä vai hyppäyksellisiä. Kirjoittajat kehittävät tilastollisia menetelmiä tämän muutoksen kuvaamiseksi ja mittaamiseksi. Kirjoittajat ensin jakoivat Euroopan yhteensä 55 valuma-alueeseen suurimpien jokisysteemien perusteella (kuva 1 ja Liite 2). Valuma-alueiden samankaltaisuutta testattiin vertaamalla alueiden vesilinnustoja keskenään perustuen lajien läsnäoloon (lajien runsauksia ei huomioitu). Tämän vertailun perusteella valuma-alueet luokiteltiin probabilistisen analyysin avulla. Analyysit tehtiin erikseen pesimälinnustolle, talvehtivalle linnustolle ja paikkalinnuille. Tutkimuksessa havaittiin jyrkkä raja Etelä- ja Pohjois-Euroopan vesilinnustojen välillä sekä pesimä- (kuva 2) että talvehtivassa (kuva 4) linnustossa. Analyysin perusteella sekä pohjoinen että eteläinen suuralue voitiin vielä jakaa osa-alueisiin pääasiallisesti pituusasteiden suuntaisia rajoja myöten siten, että Euroopan vesilinnustosta on erotettavissa yhteensä kuusi eri vesilintumaantieteellistä aluetta sekä pesimä- että talvehtimisaikaan. Paikkalinnuston osalta tulos oli hieman epäselvempi: Eurooppa jakaantui neljään suuralueeseen ja yhteensä kahdeksaan osa-alueeseen (kuva 6). Lämpötilamuuttujat luonnehtivat hyvin eri vesilintumaantieteellisten alueiden eroja. Energian saatavuus pohjoisella suuralueella rajoittaa talvilinnuston levinneisyyttä (kuva 5), kun taas kesäaikaan eteläisellä suuralueella korkeat lämpötilat voivat muodostaa stressitekijän, joka rajoittaa monien vesilintujen pesintää (kuva 3).

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Appendix 1. Waterbird presences on the breeding, wintering and resident biotic regions in Europe, and species number in each biotic region. Abbreviated supraregion names as in Fig. 2, 4 and 6.

	BREEDING						WINTERING						RESIDENCE							
	NBS		SBS				NWS			SWS			SRS							
	B1	B2	B3	B4	B5	B6	W1	W2	W3	W4	W5	W6	R1	R2	R3	R4	R5	NWRS	NBRS	NERS
Gavia stellata (Pontoppidan 1763)	1	1	1	1					1	1	1	1								
Gavia arctica (Linnaeus 1758)	1		1	1					1	1	1	1								
Gavia immer (Brünnich 1764)		1							1		1	1								
Gavia adamsii (Gray 1859)	1								1											
Tachybaptus ruficollis (Pallas 1764)	1		1	1	1	1		1	1	1	1	1	1	1	1	1	1	1		
Podiceps cristatus (Linnaeus 1758)	1		1	1	1				1	1	1	1	1	1		1	1	1		
Podiceps grisegena (Boddaert 1783)	1		1	1	1			1	1	1	1	1								
Podiceps auritus (Linnaeus 1758)	1	1	1	1					1	1	1	1								
Podiceps nigricollis Brehm 1831	1		1	1	1					1	1	1	1	1		1	1			
Fulmarus glacialis (Linnaeus 1761)	1	1	1				1		1		1		1	1				1		
Calonectris diomedea (Scopoli 1769)					1						1	1		1			1			
Puffinus puffinus (Brünnich 1764)			1		1				1	1	1	1	1	1			1			
Hydrobates pelagicus (Linnaeus 1758)			1		1				1		1	1	1	1		1		1		
Oceanodroma leucorhoa (Vieillot 1817)									1		1	1								
Sula bassana (Linnaeus 1758)	1	1	1						1		1	1	1					1		
Phalacrocorax carbo (Linnaeus 1758)	1	1	1	1	1			1	1	1	1	1	1				1			
Phalacrocorax aristotelis(Linnaeus1761)	1	1	1	1	1	1			1	1	1	1	1				1			
Phalacrocorax pygmeus (Pallas 1773)				1	1							1		1			1			
Pelecanus onocrotalus Linnaeus 1758				1	1							1								
Pelecanus crispus Brunch 1832				1	1							1					1			
Botaurus stellaris (Linnaeus 1758)	1		1	1	1					1	1	1	1	1	1	1	1			
Ixobrychus minutus (Linnaeus 1766)			1	1	1	1														
Nycticorax nycticorax (Linnaeus 1758)			1	1	1						1		1	1		1				
Ardeola ralloides (Scopoli 1769)				1	1															
Bubulcus ibis (Linnaeus 1758)			1	1	1						1	1		1		1	1			
Egretta garzetta (Linnaeus 1766)			1	1	1						1	1	1	1		1				
Egretta alba (Linnaeus 1758)				1	1						1	1		1			1			
Ardea cinerea Linnaeus 1758	1		1	1	1			1	1		1	1	1	1		1	1	1	1	
Ardea purpurea (Linnaeus 1766)			1	1	1															
Ciconia nigra (Linnaeus 1758)			1	1	1							1				1	1			
Ciconia ciconia (Linnaeus 1758)			1	1	1	1						1				1	1			
Plegadis falcinellus (Linnaeus 1766)				1	1							1								
Platalea leucorodia Linnaeus 1758			1	1	1						1	1				1				
Phoenicopterus ruber Linnaeus 1758					1						1	1		1		1				
Cygnus olor (Gmelin 1789)	1		1	1	1		1	1	1	1	1	1	1	1	1		1	1	1	
Cygnus columbianus (Ord 1815)	1						1		1											
Cygnus cygnus (Linnaeus 1758)	1	1	1	1				1	1	1	1	1						1		
Anser fabalis (Latham 1787)	1		1						1		1	1								
Anser brachyrhynchus Baillon 1833		1									1									
Anser albifrons (Scopoli 1769)	1									1	1	1								
Anser erythropus (Linnaeus 1758)	1									1		1								
Anser anser (Linnaeus 1758)	1	1	1	1	1					1	1	1	1	1	1		1			
Branta leucopsis (Bechstein 1803)											1									
Branta bernicla (Linnaeus 1758)											1									
Branta ruficollis (Pallas 1769)										1		1								
Tadorna ferruginea (Pallas 1764)				1	1					1		1			1		1			
Tadorna tadorna (Linnaeus 1758)	1		1	1	1					1	1	1	1	1	1	1	1			
Anas penelope Linnaeus 1758	1	1	1	1					1	1	1	1	1							

Appendix 1: Continued.

	BREEDING						WINTERING						RESIDENCE							
	NBS		SBS				NWS			SWS			SRS							
	B1	B2	B3	B4	B5	B6	W1	W2	W3	W4	W5	W6	R1	R2	R3	R4	R5	NWRS	NBRS	NERS
Anas strepera Linnaeus 1758	1	1	1	1	1					1	1	1	1	1	1	1	1			
Anas crecca Linnaeus 1758	1	1	1	1	1			1	1	1	1	1	1	1	1		1	1		
Anas plathyrhynchos Linnaeus 1758	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Anas acuta Linnaeus 1758	1	1	1	1	1					1	1	1	1	1						
Anas querquedula Linnaeus 1758	1		1	1	1															
Anas clypeata Linnaeus 1758	1	1	1	1	1					1	1	1	1	1	1	1	1			
Marmaronetta angustirostris (Ménétries 1832)					1							1				1				
Netta rufina (Pallas 1773)			1	1	1					1	1	1	1	1	1	1				
Aythya ferina (Linnaeus 1758)	1	1	1	1	1			1	1	1	1	1	1	1	1	1	1			
Aythya nyroca (Güldenstädt 1770)			1	1	1					1	1	1		1	1	1	1			
Aythya fuligula (Linnaeus 1758)	1	1	1	1	1			1	1	1	1	1	1	1			1	1		
Aythya marila (Linnaeus 1761)	1	1	1					1	1	1	1	1						1		
Somateria mollissima (Linnaeus 1758)	1	1	1				1	1	1		1									
Somateria spectabilis (Linnaeus 1758)	1						1		1											
Polysticta stelleri (Pallas 1769)									1											
Histrionicus histrionicus(Linnaeus1758)		1							1											
Clangula hyemalis (Linnaeus 1758)	1	1						1	1		1									
Melanitta nigra (Linnaeus 1758)	1	1	1					1	1		1	1								
Melanitta fusca (Linnaeus 1758)	1		1	1				1	1		1	1						1		
Bucephala islandica (Gmelin 1789)		1							1									1		
Bucephala clangula (Linnaeus 1758)	1		1	1			1	1	1	1	1	1	1	1				1	1	
Mergus albellus Linnaeus 1758	1			1				1	1	1	1	1								
Mergus serrator Linnaeus 1758	1	1	1	1					1	1	1	1	1							
Mergus merganser Linnaeus 1758	1	1	1	1	1		1	1	1	1	1	1	1	1				1		
Oxyura leucocephala (Scopoli 1769)				1	1							1				1				
Rallus aquaticus Linnaeus 1758	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1		
Porzana porzana (Linnaeus 1766)	1		1	1	1						1	1	1							
Porzana parva (Scopoli 1769)			1	1	1							1				1				
Porzana pusilla (Pallas 1776)			1	1	1	1						1				1				
Gallinula chloropus (Linnaeus 1758)	1		1	1	1	1	1	1	1		1	1	1	1		1	1	1	1	
Porphyrio porphyrio (Linnaeus 1758)				1	1					1		1				1				
Fulica atra Linnaeus 1758	1		1	1	1	1		1	1	1	1	1	1	1	1	1	1	1		
Fulica cristata Gmelin 1789					1							1				1				
Grus grus (Linnaeus 1758)	1		1	1							1	1								
Anthropoides virgo (Linnaeus 1758)				1																
Haematopus ostralegus Linnaeus 1758	1	1	1	1	1				1		1	1	1	1			1	1		
Himantopus himantopus (Linnaeus 1758)			1	1	1							1				1				
Recurvirostra avosetta Linnaeus 1758	1		1	1	1						1	1	1	1		1	1			
Glareola pratincola (Linnaeus 1766)				1	1															
Glareola nordmanni Fisher 1843				1																
Charadrius dubius Scopoli 1786	1		1	1	1	1						1				1				
Charadrius hiaticula Linnaeus 1758	1	1	1								1	1	1	1						
Charadrius alexandrinus Linnaeus 1758	1		1	1	1						1	1	1	1		1	1			
Charadrius asiaticus Pallas 1773				1																
Charadrius morinellus Linnaeus 1758	1		1	1	1							1								
Pluvialis apricaria (Linnaeus 1758)	1	1	1								1	1	1	1						
Pluvialis squatarola (Linnaeus 1758)	1										1	1								
Hoplopterus spinosus (Linnaeus 1758)					1															
Chettusia gregaria (Pallas 1771)				1																

Appendix 1: Continued.

	BREEDING						WINTERING						RESIDENCE							
	NBS		SBS				NWS			SWS			SRS					N W	N B	N E
	B 1	B 2	B 3	B 4	B 5	B 6	W 1	W 2	W 3	W 4	W 5	W 6	R 1	R 2	R 3	R 4	R 5	R S	R S	R S
Vanellus vanellus (Linnaeus 1758)	1	1	1	1	1	1					1	1	1	1		1	1			
Calidris canutus (Linnaeus 1758)											1	1								
Calidris alba (Pallas 1764)											1	1								
Calidris minuta (Leisler 1812)	1										1	1								
Calidris temminckii (Leisler 1812)	1		1									1								
Calidris ferruginea (Pontoppidan 1763)												1								
Calidris maritima (Brünnich 1764)	1	1							1		1	1						1		
Calidris alpina (Linnaeus 1758)	1	1	1						1		1	1	1	1						
Limicola falcinellus (Pontoppidan 1763)	1		1																	
Philomachus pugnax (Linnaeus 1758)	1		1	1							1	1	1	1						
Lymnocryptes minimus (Brünnich 1764)	1		1	1							1	1								
Gallinago gallinago (Linnaeus 1758)	1	1	1	1	1	1					1	1	1	1						
Gallinago media (Latham 1787)	1		1	1																
Gallinago stenura (Bonaparte 1830)	1																			
Limosa limosa (Linnaeus 1758)	1	1	1	1	1						1	1	1	1			1			
Limosa lapponica (Linnaeus 1758)	1										1	1								
Numenius phaeopus (Linnaeus 1758)	1	1	1	1							1	1								
Numenius arquata (Linnaeus 1758)	1		1	1	1				1		1	1	1	1				1		
Tringa erythropus (Pallas 1764)	1										1	1								
Tringa totanus (Linnaeus 1758)	1	1	1	1	1				1		1	1	1	1		1	1	1		
Tringa stagnatilis (Bechstein 1803)				1								1								
Tringa nebularia (Gunnerus 1767)	1		1	1							1	1	1							
Tringa ochropus Linnaeus 1758	1		1	1							1	1								
Tringa glareola Linnaeus 1758	1		1	1																
Xenus cinereus (Güldenstädt 1775)	1		1	1																
Actitis hypoleucos (Linnaeus 1758)	1		1	1	1	1					1	1	1	1		1				
Arenaria interpres (Linnaeus 1758)	1		1								1	1								
Phalaropus lobatus (Linnaeus 1758)	1	1		1																
Phalaropus fulicarius (Linnaeus 1758)		1									1									
Stercorarius pomarinus (Temminck 1815)	1						1	1	1		1	1								
Stercorarius parasiticus(Linnaeus1758)	1	1	1				1	1	1		1	1	1						1	
Stercorarius longicaudus Vieillot 1819	1						1		1		1									
Stercorarius skua (Brünnich 1764)		1	1						1		1	1								
Larus ichthyaetus Pallas 1773				1						1					1					
Larus melanocephalus Temminck 1820			1	1	1				1	1	1	1		1	1					
Larus minutus Pallas 1776	1		1	1			1	1	1	1	1	1								
Larus ridibundus Linnaeus 1766	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	
Larus genei Brème 1839				1	1					1	1	1			1					
Larus audouinii Payraudeau 1826												1								
Larus canus Linnaeus 1758	1	1	1	1	1		1	1	1	1	1	1	1	1				1	1	
Larus fuscus Linnaeus 1758	1	1	1		1	1	1	1	1	1	1	1	1	1			1	1	1	1
Larus argentatus Pontoppidan 1763	1	1	1				1	1	1		1	1	1	1				1	1	
Larus cachinans Pallas 1811				1	1	1				1	1	1		1		1	1			
Larus glaucoides Meyer 1822									1		1									
Larus hyperboreus Gunnerus 1767	1	1					1		1		1							1		
Larus marinus Linnaeus 1758	1	1	1				1	1	1		1	1	1	1				11		

Appendix 1: Continued.

	BREEDING						WINTERING						RESIDENCE							
	NBS		SBS				NWS			SWS			SRS					NWRS	NBRS	NERS
	B1	B2	B3	B4	B5	B6	W1	W2	W3	W4	W5	W6	R1	R2	R3	R4	R5			
Rissa tridactyla (Linnaeus 1758)	1	1	1			1	1		1		1	1	1	1				1		
Pagophila eburnea (Phipps 1774)									1											
Gelochelidon nilotica (Gmelin 1789)			1	1	1					1	1	1		1	1	1				
Sterna caspia Pallas 1770	1		1	1			1	1	1	1	1	1			1			1	1	
Sterna sandvicensis Latham 1787	1		1	1	1		1	1	1	1	1	1	1	1	1			1		
Sterna dougalii Montagu 1813			1								1	1	1							
Sterna hirundo Linnaeus 1758	1		1	1	1		1	1	1	1	1	1	1	1		1	1		1	
Sterna paradisaea Pontoppidan 1763	1	1	1				1	1	1		1	1		1				1	1	
Sterna albifrons Pallas 1764	1		1	1	1		1	1	1	1	1	1	1	1	1			1		
Chlidonias hybridus (Pallas 1811)			1	1	1							1		1		1				
Chlidonias niger (Linnaeus 1758)	1		1	1	1															
Chlidonias leucopterus (Temminck 1815)			1	1																
Uria aalge (Pontoppidan 1763)	1	1	1			1	1	1	1		1	1	1				1	1	1	
Uria lomvia (Linnaeus 1758)	1	1							1									1		
Alca torda Linnaeus 1758	1	1	1				1	1	1		1	1	1					1	1	
Cepphus grylle (Linnaeus 1758)	1	1	1				1	1	1		1		1	1				1	1	1
Alle alle (Linnaeus 1758)									1		1									
Fratercula arctica (Linnaeus 1758)	1	1	1						1		1	1	1					1		
Species number	100	54	103	97	77	17	27	37	72	50	112	121	61	60	23	41	40	39	15	3

Appendix 2. European river basins considered in the analysis. Numbers correspond to those in Fig. 1.

1. Ibero-Mediterranean
2. Guadalquivir
3. Guadiana
4. Tajo
5. Ebro
6. Duero
7. Cantabrica
8. Garonne
9. Rhône
10. Loire
11. Seine
12. Rhein
13. Shannon
14. Eastern Ireland
15. Scotland
16. Western Britain
17. Eastern Britain
18. Po
19. Tyrrhenian
20. Italo-Adriatic
21. Balkano-Adriatic
22. Danube
23. Weser
24. Elbe
25. Oder
26. Vistula
27. Ionian
28. Aegean
29. Dnestr
30. Neman
31. Western Norway
32. Glama
33. Baltic
34. Dal
35. Ljusman
36. Indals-Angerman
37. Ume
38. Skellefte
39. Pite
40. Northern Norway
41. Torne
42. Arctic
43. Western Dvina
44. Southern Finland
45. Neva
46. Beloye
47. Dnepr
48. Don
49. Volga
50. Onega
51. Northern Dvina
52. Mezen
53. Pechora
54. Northern Iceland
55. Southern Iceland