



Latitudinal trends in breeding waterbird species richness in Europe and their environmental correlates

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Abstract. We analysed the latitudinal trend in the number of breeding waterbird species in Europe using the main river basins as geographic units. The number of breeding waterbird species decreases southward, but this latitudinal trend is composed of two opposed patterns: a southward increase in the number of resident species (RS) and a southward decline in the number of aestival species (SS). Following both a bivariate and a multivariate approach, we tested nine hypotheses about the environmental causes of these trends. Using Partial Regression Analysis and Path Analysis, we found that SS richness depends on the bloom in food availability in areas with high seasonality more than on the other environmental factors; environmental stress due to an excess of energy is the second most important factor involved, whereas the third factor involved in the distribution of SS richness is competition with RS. For RS the factors involved are the climatic stability of the basins and their productivity. We also discuss the suitability of river basins as observational units in this kind of analyses and the marginal influence of their surface area in the latitudinal gradients detected here.

Introduction

Measuring species richness is one of the most suitable ways of detecting broad scale variation in biological diversity (Chown et al. 1998). Understanding how species richness is affected both locally and regionally is needed in many contexts, for example, for applied conservation purposes. In particular, any exceptional trend in generally acknowledged biogeographical patterns might potentially be useful to reveal causes that affect species richness, because the relationships between environmental and geographical factors may be different than those for typical patterns.

Avian species richness has been reported to change latitudinally, longitudinally, and altitudinally (Cook 1969; Tramer 1974; Rahbek 1997). The latitudinal trend in species richness is usually reported in the northern hemisphere as the occurrence of more species in southern areas (Pianka 1966; Stevens 1989; Rohde 1992). However, Cook (1969) and Tramer (1974) reported a southward decline in avian diversity during the breeding season in eastern North America. Cook (1969) explained the origin of this tendency as a historical consequence of the repeated Pleistocene glaciations, but Tramer

(1974) stressed that the mechanisms that maintain this pattern should also be investigated. In Europe, a southward decline in avian species richness during the breeding season has been reported specifically for waterbirds in Fennoscandia (Järvinen and Sammalisto 1976; Järvinen and Väisänen 1978; Boström and Nilsson 1983; Järvinen et al. 1987), although no general pattern has been studied on a continental scale.

Several authors have reported spatial trends in waterbird species richness on different geographical scales, from continental in Africa (Guillet and Crowe 1985) to regional (Elmberg et al. 1993) and local (Fox and Bell 1994), but not continental, in Europe. All these scales are complementary and the biogeographic processes operating on them are interdependent (Real et al. 1993). As Vaughn and Taylor (2000) pointed out, by focusing only on local habitat features and processes, such as competition and predation, many ecological studies have underestimated the contribution of regional-scale processes to local distribution patterns. This is especially important when dealing with species diversity in communities, because it depends not only on local interactions, but also on regional processes such as the dispersal of individuals between local patches, and on continental processes such as overall distribution patterns. Working on a European scale would provide a general overview of biogeographical patterns that could put studies based on regional and local scales in their appropriate context and might be helpful for establishing comprehensive conservation policies.

On a broad scale, rivers, lakes, marshes, and other wetlands are integrally linked to each other through the natural movement of water within river basins (Tucker and Evans 1997). This suggests that broad-scale biogeographical studies involving waterbirds should make use of river basins as geographical units for their analyses. Tucker and Evans (1997) pointed out that management of wetlands increasingly emphasizes integrated planning over the whole catchment basin. This, in turn, may also require analysing different taxonomic groups of waterbirds together, even if these groups are ecologically different, since the taxonomic scale must correspond to the geographic scale of variation and the integration of different types of wetlands (Hengeveld 1987). Although waterbirds include a heterogeneous group of birds, all of them depend on aquatic systems to breed and feed, respond to shallow waters, whether salt or fresh, and use water-based resources (Weller 1999). Because of this, analyses involving aquatic birds as a whole could reveal some important characteristics of the relationships between wetlands that may be helpful in the conservation of both wetlands and waterbirds.

Several processes have been hypothesized to operate on geographical trends of species richness, including the species–area relationship (Arrhenius 1921), spatial heterogeneity (Pianka 1966), environmental energy (Connell and Orias 1964), environmental favourableness–stress (Richerson and Lum 1980), productivity (Tilman 1982), and climatic stability (Klopfer 1959), among others (see Rohde (1992) for a review). In addition, the hypotheses of competition with resident species (RS) (Herrera 1978), heterospecific attraction

(Mönkkönen et al. 1990), and food availability (Herrera 1978) have been postulated specifically for birds. The interaction between different hypothesized factors can be assessed using variance partition procedures (see, e.g., Boone and Krohn 2000).

In this work we tried to check whether the reported southward decline in breeding waterbird species richness in Fennoscandia is part of a general trend in Europe. We also tested the above-mentioned nine environmental hypotheses about the causes of the latitudinal trends of waterbird species richness in Europe, using the main river basins as geographic units.

Material and methods

The species and the study area

We considered the 154 indigenous waterbird species that breed in continental Europe, the British Isles, and Iceland. We denominate as waterbirds the swimming, diving, or wading birds that belong to the orders Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Phoenicopteriformes, Anseriformes, Gruiformes, and Charadriiformes. We included seabirds because many of these frequently breed in both marine and fresh-water environments, and because the inland dynamics of rivers affect production levels in coastal breeding areas (Mann and Lazier 1991; Tucker and Evans 1997; Olivero et al. 1998).

We took the breeding distribution of the species in the 55 main river basins of Europe from Cramp and Simmons (1977, 1980, 1983), Cramp (1985), and Hagemeyer and Blair (1997), 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. (1983), Álvarez et al. (1985), Elosegui (1985), Devillers et al. (1988), Peris and Carnero (1988), Rufino (1989), Urios et al. (1991), Brichetti et al. (1992), Ceballos and Guimerá (1992), Gibbons et al. (1993), and Purroy (1997). Some of these sources delineate occurrence using free-drawn maps whereas others use grid-based systems; we considered a species to be present in a basin if the drawing of the breeding area affected the basin or a square where breeding was reported was included into it.

We used river basins as geographic units because the topography, water availability, and evapotranspiration of basins strongly affect wetlands (Real et al. 1993; Tucker and Evans 1997). River basins are especially suitable for studies on waterbirds because they integrate different ecosystems by the interchange of water, energy, sediments, and nutrients among wetlands (Laut et al. 1975; Austin and Margules 1986). Besides this, river flows affect the nutrient enrichment of coastal waters near the river mouths (Mann and Lazier 1991; Lalli and Parsons 1993), thus affecting the breeding of birds throughout the coast (Hay 1992). In this way, some processes potentially affecting waterbird

species richness are conditioned by watersheds and may only be assessed using whole river basins as observational units (see, for example, Real et al. (1993) and Chase and Leibold (2002)).

We measured species richness using the number of species present in each basin. This is the simplest index of species diversity and weighs rare and common species equally, a suitable condition for measuring species richness in a situation with many rare, but regular species (Pianka 1966), as is the case here.

Hypotheses and variables

The total pool of species that breed in a river basin is composed of two types of species, namely RS, which maintain populations within the basin all over the year, and aestival species (SS), which are present in the basin only during the breeding season after migrating from elsewhere. Many hypotheses addressing broad-scale spatial variation in species richness may be referred to either group of species. However, avian migration and residence have some peculiarities due to which some hypotheses about the causes of geographic trends in species richness have been proposed specifically for one situation or the other. Consequently, we divided the total number of breeding waterbirds of each basin into RS and SS, and tested the following hypotheses for explaining the distribution of RS and SS in Europe during the breeding season.

Hypotheses for both RS and SS

Area (Arrhenius 1921; Connor and McCoy 1979). The number of species is higher in larger areas as compared with smaller ones. Associated variable: area of the basin (A). Prediction: a direct relationship between species richness and A (see also Lomolino 2001).

Spatial heterogeneity (Pianka 1966). The more heterogeneous and complex the physical environment is, the more diverse and complex the communities that inhabit it will be. Associated variables: range of elevation (ER) and spatial range of temperature of July (STJ, which is the difference in the mean temperature of July (TJ) between the two localities with the most extreme values within a river basin). Prediction: a direct relationship between species richness and the associated variables.

Environmental energy (Connell and Orias 1964). The species number is limited by the available energy (see also Gaston 2000). Associated variables: mean annual temperature (T), mean potential evapotranspiration (PET), and TJ. Prediction: a direct relationship between species richness and either T , PET, or TJ.

Environmental favourableness-stress (Richerson and Lum 1980). Species richness is favoured when the mean values of the environmental variables lie

within the optimal range for the physiological needs of the species. Associated variables: T , PET, and TJ. Prediction: an inverse relationship between species richness and the associated variables would be indicative of environmental stress due to an excess of energy, and a unimodal relationship between species richness and either T , PET or TJ would be indicative of favourableness-stress (Olivero et al. 1998).

Productivity (Tilman 1982). Over a range of resources that goes from extremely poor to low, the number of species will increase along with the resources, within a range of moderate resources species richness will be maximum, and it will decrease as the resources become more abundant. Associated variables: mean annual precipitation (P) and actual evapotranspiration (AET). Prediction: in accordance with Mittelbach et al. (2001), we tested for a direct, inverse or unimodal response of species richness to the associated variables.

Hypotheses for SS

Competition with RS (Herrera 1978). The decreasing proportion of migrant birds breeding to the south would be due to interspecific competition with RS. Associated variable: number of RS per basin. Prediction: an inverse relationship between SS richness and RS.

Heterospecific attraction (Mönkkönen et al. 1990). Migrant birds could use RS as cues for 'good' breeding sites, so the number of breeding SS will be higher in basins with higher number of RS. Associated variable: RS. Prediction: a direct relationship between SS richness and RS.

Food availability (Herrera 1978). Seasonal blooms of insect prey increase the food availability in climatically unstable environments with short summer growing seasons and harsh winters, thus allowing more species to exploit it during the breeding season. As insects are at the base of the food chain they may contribute, directly or indirectly, to the diet of waterbird adults and chicks. Associated variable: temperature range (TR). Prediction: a direct relationship between SS species richness and TR.

Hypothesis for RS

Climatic stability (Klopfer 1959). A climatically stable environment will permit the coexistence of more niches with predictable resources on which rare species can specialise and, therefore, will favour an increase in species richness (Brown and Lomolino 1998); in addition, more species will be able to reside in climatically stable basins, as it will be easier for their physiological constraints to tolerate the annual environmental changes. Associated variable: TR. Prediction: an inverse relationship between RS richness and TR.

We obtained P , T , TR, STJ, and TJ values from the Climatic Atlas of Europe (1970); PET and AET from the maps of the USSR National

Committee for the International Hydrological Decade (1977); and ER, *A*, and latitude (LA) from the Times Atlas of the World (1988).

Statistical methods

We performed a Kolmogorov–Smirnov test on each variable to check their normality. To assess the latitudinal trend in species richness we correlated the mean latitude of each basin with the breeding waterbird species richness (*S*), RS richness, SS richness, and the environmental variables, using Pearson's correlation coefficient with normal variables and Kendall's correlation coefficient with non-normally distributed ones. We only tested the hypotheses whose associated variables were significantly correlated with latitude, since we wanted to explain the latitudinal trend in species richness. Factors that do not co-vary with latitude may affect waterbird species richness, but they cannot be invoked as causes of a latitudinal tendency in species richness.

We first tested each hypothesis separately relying on bivariate analyses because stepwise variable selection techniques – although capable of revealing complex relations between environmental factors – make some questionable assumptions and their results sometimes have doubtful biological validity (James and McCulloch 1990; Chown et al. 1998). We performed linear regressions to detect predicted monotonic responses (either direct or inverse) of the species richness (RS or SS) to each variable analysed. We also performed second-degree polynomial regressions to detect predicted unimodal responses of RS and SS to the variables *T*, PET, TJ, *P*, and AET, and we located the maximum with respect to the independent variables to check the unimodality of the response. To prevent the increase of the type II error that may be caused by the testing of several hypotheses simultaneously, we used Bonferroni's sequential test (Rice 1989), starting with a significance level $\alpha = 0.05$ divided by the number of hypotheses.

Following this, and to explain RS and SS by a combination of several hypotheses, we performed a stepwise multiple regression of the species richness on the variables that remained significant after applying the above-mentioned Bonferroni test (James and McCulloch 1990). The significant bivariate polynomial functions were included in the multiple regression analyses as if they were linear variables, and the resulting models were compared using the *F*-ratio test, in which the polynomial functions consumed two degrees of freedom each. In this way, we were able to select a subset of latitudinally oriented environmental variables that significantly explained the distribution of RS and SS in Europe according to the predictions of the explanatory hypotheses. We considered that the selected variables sufficiently explained the latitudinal trend in species richness if the partial correlations between RS and LA and between SS and LA were non-significant after controlling for those variables.

If we obtained more than one hypothesis combined in the multiple regression equations, then we used the selected variables in the variance partitioning

procedure called Partial Regression Analysis (Legendre 1993). The aim of this analysis is to specify which part of the total variance in species richness explained by the multiple regression (R_T^2) is due to each selected hypothesis exclusively (R_{Hi}^2), and which parts are due to the interaction between pairs of hypotheses (R_{Hij}^2) and between all the selected hypotheses together (R_{It}^2).

For performing the Partial Regression Analysis, we regressed in turn each selected environmental variable related to one hypothesis onto the subset of selected variables related to other hypotheses, and the regression residuals were retained. The residuals, which represent the part of the variation explained by one hypothesis that is not explained by the other hypotheses, were then used to model the target variable (RS or SS). We assessed the pure effect of each hypothesis (R_{Hi}^2) by regressing the species richness on the residuals related to the hypothesis involved. The combined effect attributable exclusively to each pair of hypotheses (R_{Hi+Hj}^2) can also be computed by multiple regression of the species richness on both subsets of residuals combined. The variation due to the interaction between pairs of hypotheses (R_{Hij}^2) was obtained by subtracting from R_{Hi+Hj}^2 the pure effect of the two hypotheses ($R_{Hi}^2 + R_{Hj}^2$) involved. The variation due to the interaction between all the hypotheses (R_{It}^2) was obtained by subtracting from R_T^2 the pure effect of the selected hypotheses and the effect of the interaction between pairs of hypotheses. The unexplained variation of the species richness is $1 - R_T^2$.

Finally, to obtain a comprehensive view of the factors involved in the latitudinal trend in breeding waterbird species richness in Europe, we used the significant multiple regression equations obtained for RS and for SS to make a path diagram of the hypothetical relationships that yielded the total number of species in each European basin. We assessed these relationships using Path Analysis.

Results

The distribution of the number of breeding waterbird species, RS, and SS on the European river basins can be seen in Figure 1. The Kolmogorov–Smirnov test showed that all the variables, except *A*, had normal distributions. The number of breeding waterbird species (*S*) was positively correlated with latitude ($r = 0.500$; $p < 0.001$), that is, the number of species decreases southward. However, RS was negatively correlated with latitude ($r = -0.508$; $p < 0.001$) while SS was positively correlated with it ($r = 0.689$; $p < 0.001$), that is, there is a southward increase in the number of RS and a southward decline in the number of SS. All variables but *A* and *P* were significantly correlated with LA (Table 1). Accordingly, the hypothesis of area and the variable *P* in the productivity hypothesis were excluded from the following analyses.

On the basis of the bivariate approach (Table 2), the distribution of RS richness was significantly explained by the hypotheses of climatic stability (inverse relation with TR), environmental favourableness-stress (unimodal

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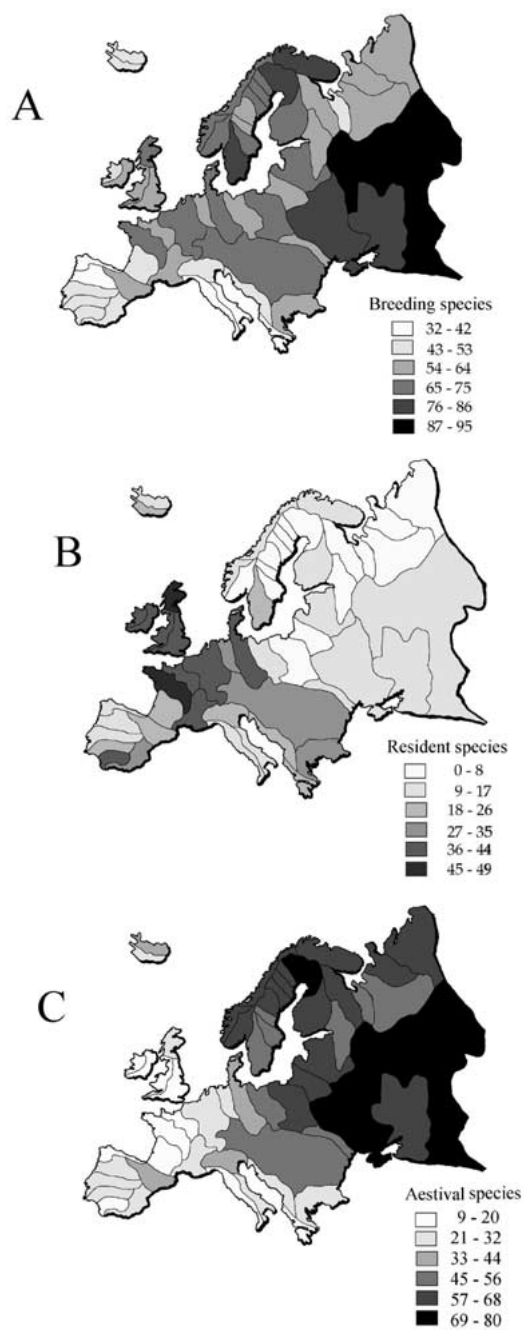


Figure 1. Species richness of breeding waterbirds (A), RS (B), and SS (C) in the European river basins.

Table 1. Values of Kendall's (for the variable *A*) and Pearson's correlation coefficients between latitude (LA) and the environmental variables. See text for abbreviations. * $p < 0.05$; ** $p < 0.01$.

<i>A</i>	ER	STJ	<i>T</i>	PET	TJ	<i>P</i>	AET	RS	TR
−0.011	−0.454**	−0.329*	−0.966**	−0.950**	−0.847**	−0.101	−0.777**	−0.508**	0.455**

Table 2. Bivariate regression equations of RS and SS on the environmental variables that were significant ($p < 0.01$) after applying Bonferroni's sequential test and which were in accordance with the responses predicted by the hypotheses. See text for abbreviations.

RS = 54.778 − 1.754TR	$R^2 = 0.524$
RS = 3.606 + 3.776 <i>T</i> − 0.152 <i>T</i> ²	$R^2 = 0.434$
RS = 6.538 + 1.792 <i>T</i>	$R^2 = 0.374$
RS = −12.648 + 0.067AET	$R^2 = 0.256$
RS = −30.376 + 0.129PET − 0.00007PET ²	$R^2 = 0.210$
SS = −14.781 + 2.776TR	$R^2 = 0.683$
SS = 62.127 − 1.061RS	$R^2 = 0.586$
SS = 63.177 − 3.072 <i>T</i>	$R^2 = 0.572$
SS = 70.960 − 0.042PET	$R^2 = 0.340$
SS = 90.406 − 0.103AET	$R^2 = 0.313$

relation with *T* and PET), energy (direct relation with *T*), and productivity (direct relation with AET), whereas the distribution of SS richness was significantly explained by the hypotheses of food availability (direct relation with TR), competition with RS (inverse relation with RS), environmental stress (inverse relation with *T* and PET), and productivity (inverse relation with AET).

The stepwise multiple regression analysis yielded the following equations:

$$RS = 33.255 - 1.505 TR + 0.035 AET; \quad R^2 = 0.583; \quad p < 0.001 \quad (1)$$

$$SS = 30.275 - 0.023 PET + 1.709 TR - 0.406 RS; \quad R^2 = 0.828; \quad p < 0.001 \quad (2)$$

On the basis of this multivariate approach, the best hypotheses were those of climatic stability (inverse response of RS to TR) and productivity (direct response of RS to AET) for RS, and environmental stress (inverse response of *S* to PET), food availability (direct response of SS to TR), and competition with RS (inverse response of SS to SR) for SS. The partial correlation between RS and LA after controlling for TR and AET was non-significant ($R_{RS/LA,TR \ AET} = -0.0528$, ns), as was also the case with the partial correlation between SS and LA after controlling for PET, TR and RS ($R_{SS/LA,PET \ TR \ RS} = 0.1042$, ns). Because of this, we considered that the latitudinal trends in RS and SS were sufficiently accounted for.

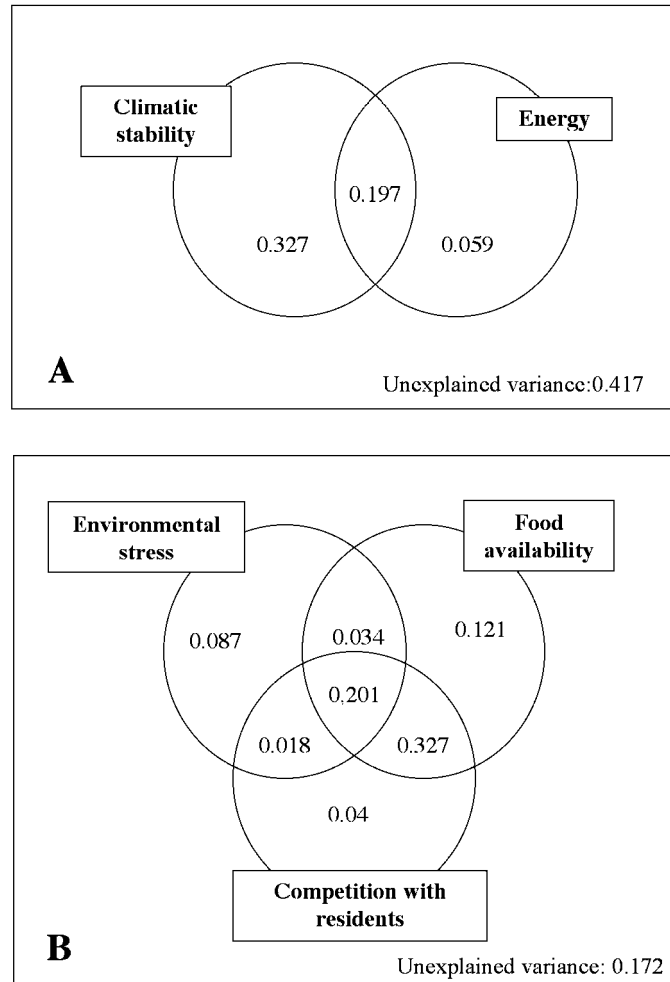


Figure 2. Results of the variance partitioning using Partial Regression Analysis. Values shown in the diagrams are the proportion of RS richness (A) and SS richness (B) explained by each environmental hypothesis and their interactions.

According to the Partial Regression Analysis, the explanation of the geographical variation of waterbird species richness during the breeding season was divided into parts as follows (Figure 2):

For RS:

- (1) the specific effect attributable to the hypothesis of climatic stability after the effect attributable to the hypothesis of productivity is partialled out (R^2_{H1}): 0.327;

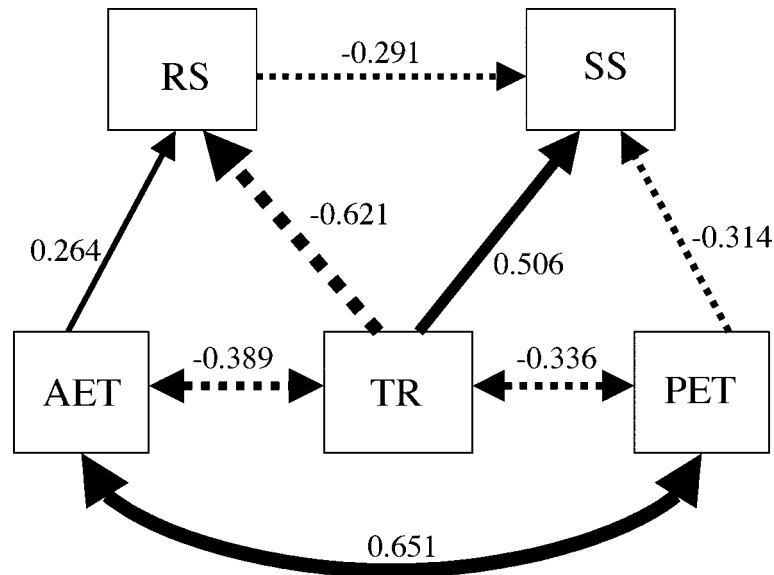


Figure 3. Standardised regression weights resulting from Path Analysis. Simple arrows are based on all the relationships included in the multiple regression equations obtained for SS and for RS. Double arrows indicate the correlations between the environmental variables. See text for abbreviations.

- (2) the specific effect attributable to the hypothesis of productivity after the effect attributable to the hypothesis of climatic stability is partialled out (R_{H2}^2): 0.059;
- (3) the specific effect attributable to the interaction between climatic stability and productivity (R_{I12}^2): 0.197;
- (4) unexplained variation: $1 - 0.583 = 0.417$.

For SS:

- (1) the specific effect attributable to the hypothesis of food availability after the effects attributable to the other two hypotheses are partialled out (R_{H1}^2): 0.121;
- (2) the specific effect attributable to the hypothesis of environmental stress after the effects attributable to the other two hypotheses are partialled out (R_{H2}^2): 0.087;
- (3) the specific effect attributable to the hypothesis of competition with RS after the effects attributable to the other two hypotheses are partialled out (R_{H3}^2): 0.040;
- (4) the specific effect attributable to the interaction between food availability and environmental stress after the effects attributable to competition with RS are partialled out (R_{I12}^2): 0.034;

- (5) the specific effect attributable to the interaction between food availability and competition with RS after the effects attributable to environmental stress are partialled out (R_{I13}^2): 0.327;
- (6) the specific effect attributable to the interaction between environmental stress and competition with RS after the effects attributable to food availability are partialled out (R_{I23}^2): 0.018;
- (7) the specific effect attributable to the interaction between the three selected hypotheses (R_{It}^2): 0.201;
- (8) unexplained variation: $1 - 0.828 = 0.172$.

Figure 3 shows the path diagram that results from the combination of the relationships included in the regression Equations 1 and 2, as well as the assessment of these relationships by Path Analysis.

Discussion

The number of breeding waterbird species decreases southward in Europe, but this latitudinal trend is composed of two conflicting patterns; a southward increase in the number of RS and a southward decline in the number of SS. The latitudinal trend in RS richness is consistent with the pattern reported for most groups of species (Pianka 1966; Rohde 1992). However, the latitudinal trend in SS contradicts this common pattern, and the fact that the patterns for both RS and SS intertwine in Equation 2 complicates the overall view of the situation.

However, the number of RS, being a component of the total number of breeding species, was not significantly correlated with it ($r_{S-SR} = -0.068$, ns). This seems to indicate that the role of the number of RS is not apparent unless its effect on the number of SS is taken into account. Cartron et al. (2000) pointed out that when some of the relations among multiple variables are negative, the possibility exists that the effect of a factor is obscured by another, stronger factor through interrelationships between variables. From a mathematical perspective, limits on the magnitude of covariation can arise due to the positive semi-definite (PSD) criterion, which is a property of all correlation matrices that constrains all eigenvalues and the determinant of each principal minor in a correlation matrix to values greater than or equal to zero (Cartron et al. 2000).

In a system with three variables, one implication of the PSD criterion is that, if two correlations are positive and one negative, the expected relationships may not all be observed following a bivariate approach. This is the case with the relationship between *S*, RS, and SS, as RS and SS make up the total number of breeding waterbird species but have a negative relationship between them. Because of this, their roles in the latitudinal trend of breeding species richness are reciprocally obscured. Since the number of RS is lower than that of SS, RS is the variable whose effect is most obscured, even causing the correlation between RS and *S* to be negative. Notwithstanding this, the combination

of five different hypotheses, two for RS and three for SS, seems to provide a satisfactory environmental explanation of the mechanisms that maintain their latitudinal patterns, as opposed to those that historically originated these patterns (see Cook 1969 and Tramer 1974).

As regards the possible effect of area on waterbird species richness, it is unlikely to have any significant impact on the observed latitudinal trends. Not only is area not correlated with latitude, but Figure 1 shows that northernmost basins, which support more SS, are not larger than southern basins, and that the river basins supporting more RS clearly are not the largest ones. Four of the 55 river basins (Volga, Don, Dnepr and Danube) are larger than usual, but this seems not to affect the distribution of RS richness, and only may have a marginal statistical effect for SS contributing to a longitudinal rather than latitudinal trend in species richness.

The effect of food availability

SS richness in Europe depends on seasonality more than on other environmental factors. Seasonality has been related with the availability of insects during summer. Turner et al. (1988) found that the diversity of lepidopteres is higher in areas with higher differences in temperature between the coldest and the warmest months. They interpreted this as a consequence of diapausing insects expending but not consuming energy, and thus being adversely affected by mild winters that raise their metabolic rate and deplete their reserves. Herrera (1978) pointed out that more migrant species might breed in areas with sharp differences between the summer and winter conditions, because in these environments seasonal blooms of insect prey increase the total food availability during the breeding season. The same idea was put forward for southern African waterbirds by Guillet and Crowe (1986), who suggested that ephemeral aquatic biotopes usually fed by wadis and other non-permanent rivers generate a short-term flush of food that is readily exploited by migrants. Thus, their results are consistent with the hypothesis that migrant birds use a periodical super-abundance of food and/or habitat that cannot be utilised fully by RS. In the same way, Järvinen and Väisänen (1980) suggested for Finnish land birds that their ability to migrate makes it easier for them to make use of the pronounced seasonal changes of resource levels in the north of Europe (see also MacArthur 1959; Willson 1976; Herrera 1978). This could be one of the clues to migration, with birds going to the places with more food available during the breeding season, when they need to feed their chicks as well as themselves (Cox 1985).

The effect of environmental stress

Environmental stress due to an excess of energy is the second most important factor involved in the distribution of SS richness in Europe. Areas with higher

values of energy have been proposed to be environmentally stressful for the species with a thermoregulation system that develops earlier (Beintema and Visser 1989). Koskimies and Lathi (1964) suggested that an earlier development of thermoregulation implies a higher energy intake and a high metabolic rate that can cause physiological problems in areas with warm weather. Authors such as Beintema and Visser (1989) and Olivero et al. (1998) considered, for example, that this could be the reason for the Scolopacidae to be more restricted to the north of Europe than the Charadriidae, which have poorer thermoregulation, longer dependence on brooding, and slower development. Given that the number of Scolopacidae is higher than the number of Charadriidae in Europe, environmental stress may eventually exert an overall influence on SS richness on a continental scale.

The effect of competition with RS

The third hypothesis involved in the distribution of SS richness is competition with RS. Herrera (1978) found a decreasing proportion of migrant birds breeding in southern Europe and attributed it to a possible interspecific competition with RS. Böhning-Gaese and Bauer (1996) suggested that this effect is more focused on long distance migrants, which might suffer from competition with populations of RS and short-distance migrants. Our results are consistent with this idea, as some species here considered to be RS in a basin are short-distance migrants whose populations are replaced in the basin, while all long-distance migrants are SS.

The effect of climatic stability

The distribution of RS richness is mainly determined by the annual temperature stability. Klopfer (1959) proposed that a stable environment might enhance faunal species diversity by allowing space for more niches, because the type of cover, nesting sites, and food which are available are less variable and the range of environmental variation to which a species has to respond could be decreased as compared with the range required of a species residing in a seasonally more variable area. This could favour particularly the presence of rare species that may depend on scarce but predictable resources (Brown and Lomolino 1998), thus contributing to increase species richness. In addition, in stable areas selection could favour the development of responses to a narrow range of stimuli in the members of local fauna over migratory behaviours, thus increasing the number of species that reside in the basin all over the year.

The effect of productivity

The second factor involved in the distribution of RS in European river basins is productivity. However, the relation between these species and productivity is

not unimodal but direct. This might mean that the mechanisms invoked to explain the inverse slope of the relationship predicted by Tilman (1982), particularly that higher productivities will reduce spatial heterogeneity in the relative supplies of different resources, thus reducing the number of species able to coexist, are not acting on the European RS. It is possible that the range of productivity that goes from moderate to extremely high is absent from Europe in winter due to the lack of high temperatures. This might cause the absence of an inverse slope in the relationship between RS and productivity, which would also suggest that the conditions of the winter are more important than those of the summer in affecting the number of RS in the European river basins. To explain the direct productivity–diversity relationship, Abrams (1995) proposed that increased productivity can cause diversity to increase monotonically by (a) raising the abundance of rare species, thus reducing their extinction rates; (b) increasing the abundance of rare resources or combinations of resources and conditions that are required by specialist species; and (c) increasing intraspecific density dependence, thus allowing coexistence of species, some of which would be excluded at lower productivity.

Chase and Leibold (2002) showed that productivity–diversity patterns are scale-dependent in watersheds, with a unimodal relationship among ponds but a positively linear response among watersheds. They explained this scale-dependence by the positive correlation between productivity and species dissimilarity between ponds within the watershed. If a similar mechanism is working for the European RS, then dissimilarity between species composition in different wetlands should be higher within river basins of higher productivity.

Interactions between explanatory factors

The bivariate and multivariate approaches revealed some inconsistencies about the possible causes of the distribution of waterbird species richness. Productivity, for instance, was a significant factor for SS according to the bivariate approach, but not according to the multivariate analysis. This may indicate that the apparent role of productivity was a spurious effect of the correlation of AET with other environmental variables that affect SS richness more directly. In fact, AET is significantly correlated with PET ($r = 0.651$, $p < 0.001$), SR ($r = 0.506$, $p < 0.001$), and TR ($r = -0.389$, $p < 0.01$).

On the other hand, the effects attributable to the interactions between different factors indicate that these factors provoke the same response in the target variable. For instance, for SS the effects of food availability and competition with RS operate in the same direction, that is, the relationship is positive between RT and SS, negative between RS and SS, and also negative between RT and RS. This tends to overestimate the individual effects of food availability and competition with RS on SS richness; because of this, their relative importance is better assessed taking into account their pure specific effects.

The overall pattern resulting from all different factors affecting waterbird diversity and their interactions is quite complex. As Whittaker et al. (2001) stressed, many disparate phenomena must be taken into account to explain macro-scale patterns of species richness. Figure 3 is an attempt to integrate these factors affecting breeding waterbird diversity into a single explanation model.

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