

Aspects of heterogeneity in the distribution of diversity of the European herpetofauna

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Abstract

In the western Palearctic, species richness decreases with increasing latitude for amphibians and reptiles. Hotspots are found in the southernmost parts of the area for reptiles, while for amphibians they are in western middle latitude parts. Rapoport's rule predicts that species range increases with latitude and that hotspots contain many species of small range. Both predictions are upheld in the case of reptiles, but the hotspots for amphibians contain mostly widespread species. Most amphibian species of small range are found in southern areas. The seasonal climatic variation hypothesis that has been proposed as an explanation for Rapoport's rule is not verified for the Palearctic herpetofauna.

Keywords: Species richness, hotspots, distribution range, Rapoport's rule, western Palearctic, reptiles, amphibians.

Résumé

La richesse des espèces de reptiles et d'amphibiens diminue en fonction de l'accroissement de la latitude dans la région Paléarctique occidentale. Les aires les plus riches en reptiles se situent dans les parties les plus au sud de la région, tandis que les amphibiens abondent dans les moyennes latitudes occidentales. La règle de Rapoport prévoit que l'aire d'une espèce augmente en fonction de la latitude et que les aires les plus riches en espèces contiennent plusieurs espèces de faible extension géographique. Les deux prévisions sont acceptées pour les reptiles, tandis que les aires riches en amphibiens contiennent surtout des espèces de grande extension géographique. La plupart des amphibiens de faible extension se trouvent dans les parties sud de la région étudiée. L'hypothèse de variation climatique saisonnière, proposée comme une explication de la règle de Rapoport, n'est pas vérifiée dans le cas de l'herpétofaune paléarctique.

INTRODUCTION

One of the earliest and most striking findings of modern conservation biology is that the old (and sometimes unanswered) theoretical questions in ecology and biogeography are crucial for the understanding of the maintenance of biological diversity. For instance, the question "why does one find a given number of species in a given environment" (MAY, 1996) has important applications in conservation biology. Furthermore, the understanding of the spatial variability in species richness is of a high

value for conservation planning because it fashions and elucidates two major questions: "how many species are in a given environment or area", and "how great is the variation of species richness among environments or areas"?

The spatial distribution of biodiversity is heterogeneous. The latitudinal diversity gradient, from the species-poor high latitudes to the hyperdiverse tropics, is a well documented biogeographical pattern for many groups (for review, *e.g.* STEVENS, 1989), with a general tentative explanation involving mainly climatic stability, extreme biological specialization and niche division (EHRlich & WILSON, 1991).

Beyond the biological considerations of the potential factors influencing the presence of species and species richness, the fact is that the number of species in an area is the result of the overlapping geographic distribution of individual species. One important challenge in conservation biology is to identify, on various spatial scales, those areas featuring exceptional concentrations of species. These areas qualify as hotspots (MYERS, 1988, 1990). However, the definition of a hotspot *per se* is of little practical value for conservation purpose. What really matters is the level of biodiversity congruence between the hotspots of different groups of organisms (GASTON, 1996), and the existence of a positive relationship between diversity and rarity within the hotspots.

MYERS (*op. cit.*) performed hotspot analysis on a global scale, in which he identified 18 large areas as hotspots located in low latitudes (the tropics and the Mediterranean type bioclimatic areas). These findings agree with the latitudinal diversity pattern of species richness, and indirectly suggest a geographic coincidence of global hotspots for plants, mammals, birds, reptiles, etc. On a continental scale quite a few studies on the distribution of the species richness of various taxa have been carried out, especially for N. America (SCHALL & PIANKA, 1978; CURRIE & PAQUIN, 1987; CURRIE, 1991; PAGEL *et al.*, 1991), Australia (SCHALL & PIANKA, 1978; PIANKA & SCHALL, 1981; SMITH *et al.*, 1994), and Europe (ADAMS & WOODWARD, 1989; LETCHER & HARVEY, 1994). The general latitudinal gradient in species richness has been verified in most of these studies (N. America and Europe though not Australia). At this crude spatial resolution, data on the geographic coincidence of hotspots for different taxonomic groups are very few and rather conflicting in the sense of affirming a general pattern. Comparing species richness distribution maps within individual continents, WILLIAMS & GASTON (1994) argued that the areas of maximal richness for different taxonomic groups do not coincide. GASTON & DAVID (1994), using a null model of hotspot distribution across Europe (*i.e.* hotspots were distributed across grid cells at random) of twelve higher taxa of animals and plants, demonstrated that a greater number of areas containing several individual taxa hotspots than expected by chance occur in this continent.

The existence of numerous species in a hotspot area may result from the presence of many species of narrow distribution range ("rare" or "endemic" or "scarce" as MYERS claims) but may also result from the coexistence of widespread species (these two situations are not mutually exclusive). The assumption of MYERS cannot be generalized to any scale, as the knowledge and the perception of the distribution of species richness, of individual species distribution, and of the coincidence of the range of different species are certainly scale-dependent. As an example, on a regional scale, in the British Isles, it has been shown that rare or scarce species are not necessarily found in hotspot areas (PRENDERGAST *et al.*, 1993). An analysis by CURNUTT *et al.* (1994) comparing Australian avifauna hotspots with the results of PRENDERGAST *et al.*

(*op. cit.*) on British avifauna hotspots indicates that rare species and hotspots tend to become more coincident at progressively coarser scales of resolution, because areas become species-rich after the addition of a "pool" of rare species.

On a continental scale the relationships between species range, species richness and latitude can be considered within the theoretical context of a hypothesis formulated by STEVENS (1989), which is called Rapoport's rule. This hypothesis is based on the pattern that arises from the relation between the geographical range of species and the mean latitude of its range. The general pattern is that species richness increases with declining latitude, while the size of species range declines. The proposed explanation to this phenomenon is that at higher latitudes individual organisms have to cope with a wide range of climatic conditions in comparison with the organisms found at lower latitudes. This fact has caused the evolution of broad climatic tolerances in high-latitude species, which makes them capable of having a wider distribution range.

The purpose of this paper is to investigate some aspects of the heterogeneity in the distribution of species richness on a continental scale in Europe. We use amphibians and reptiles as a model to answer the following questions: (a) Is the latitudinal pattern of species richness verified in the case of the European herpetofauna? (b) Where are the hotspots located and do reptile and amphibian hotspots coincide? (c) Does Rapoport's rule hold for the European herpetofauna? and (d) Is the climatic explanation to Rapoport's rule demonstrated in this area?

Since a latitudinal gradient in species richness is pre-supposed, the acceptance of Rapoport's rule implies that besides the positive latitude-species range relationship, there is a general coincidence of hotspots for the various taxonomic groups at low latitude areas. Moreover, the hotspot areas have species of narrow range. This deduction is going to be a basic criterion for checking Rapoport's rule in this study.

MATERIALS AND METHODS

Grid cell size

The geographic area under investigation is part of the western Palearctic. It includes the whole European region and part of Asia (Turkey and the Caucasian region) (fig. 1). Numbers of reptile and amphibian species and climatic variables (see below) per unitary surface of the study area were the basic biogeographic descriptors necessary to examine the above mentioned questions. The area has been divided into 188 quadrats which follow lines of latitude and longitude, a method often used in similar studies (*e.g.* SCHALL & PIANKA, 1978; CURRIE & PAQUIN, 1987; ADAMS, 1988). Because meridians converge towards the poles and in order to get quadrats of similar size, the sampling grid that we used had the following characteristics: the height of each quadrat was set to 2.5° of latitude whilst the width was set differently in three distinct zones: (a) in the first zone, from 60° N to 70° N, the quadrat width was 5°, (b) in the second zone, from 50° N to 60° N, the quadrat width was 3.75°, (c) in the third zone, from 34° N to 50° N, the quadrat width was 2.5° (fig. 1). The areas of the quadrats vary from about 40,000 km² to 60,000 km², with a mean of about 50,000 km².

Islands were treated separately because they tend to have a smaller number of species with a higher proportion of endemics in comparison to continental areas. Since we were interested in large scale patterns of species richness, we excluded all islands except for the six largest (Ireland, Corsica, Sardinia, Sicily, Crete and Cyprus). For these six islands quadrats that would have included parts of both island and mainland were shifted or enlarged so that they included only entire islands.



FIG. 1. – The area under investigation and the geographic delineation of the 188 quadrats defined by the sampling grid.

For each quadrat, species richness of reptilian and amphibian fauna was calculated by overlaying distribution maps of individual species on the grid map and by summing the number of species occurring in each quadrat. Basic distribution maps were contained in the *Atlas of European Reptiles and Amphibians* (Societas Europaea Herpetologica, *in press*). The basic data sets produced using the Atlas were improved in those cases in which there was incomplete sampling (Russian region) or for areas exempted from coverage (Turkey and Causasian region). In these cases, additional information was found in *Lurche und Kriechtiere Europas* (ENGELMANN *et al.*, 1985), and in the *Handbuch der Reptilien und Amphibien Europas* (BOHME, 1981-1992).

Some error could be introduced because of the unequal size of the quadrats. Using the species number – area relationship, it is possible to estimate a theoretical value of species number for each quadrat if all quadrats were of an equal size. We use Preston's equation, $S = c \cdot A^z$, to get an estimate of the difference in the number of species that could be due to the unequal size of quadrats. If S_1 is the number of species found in a quadrat with an area equal to A_1 and S_2 the number of species that the same quadrat would have if its area were equal to the mean value A of the land area of all quadrats (excluding the six islands) then S_1/S_2 equals $(A_1/A)^z$ and the percentage change in the species number of each quadrat equals $(1 - (A/A_1)^z) \cdot 100$. A reasonable range for z (for continental areas) is 0.12-0.17 (BLONDEL, 1995). We select 0.17 for our calculations to estimate the maximum possible error.

There is no significant correlation between the land area within each quadrat and the number of species it contains. The correlation coefficients between species richness and land area of each quadrat is $r = 0.01$ for reptiles and $r = 0.02$ for amphibians. We estimate that in only seven quadrats the number of reptile species would change (increase or decrease) by more than 1.5 species (maximum change : +3.3 species) if all quadrats were equal. For amphibians this happens in three quadrats (maximum change: +2.4 species). The greatest deviation is observed in species-rich quadrats whose land area is significantly larger or smaller than the mean. In the case of amphibians the error would be expected to be less because of the smaller number of amphibian species in general. A change greater than 10% in the species number is observed in seven quadrats while a change greater than 5% is observed in 20 quadrats. The degree of error is negligible and no correction of the grid was considered necessary.

Descriptors

The climatic variables that were used as descriptors of environmental variability for each quadrat were annual temperature range (difference between highest and lowest monthly temperatures) and annual range of precipitation (difference between highest and lowest monthly precipitation) divided by the total annual precipitation. We also tried the standard deviation of monthly temperatures and precipitation as alternative measures of climatic variability. However, these two variables were found to be very highly correlated with temperature and precipitation range respectively ($r > 0.99$ in both cases).

During certain times of the year, when environmental conditions are unfavourable, most species of reptile and amphibian are inactive. For this reason we calculate seasonal variability both during the whole year but also during the season in which these organisms are expected to be active. Adaptation to local conditions is also to be taken into account: species or populations inhabiting northern areas may be more cold-tolerant than those in southern areas. Thus, for amphibians the active season is taken to be the months in which the mean monthly temperature exceeds 5°C while for reptiles the active season is taken to be the months in which the mean monthly temperature exceeds 10°C for the northern half of Europe (grid cells north of the 47.5° parallel) and 15°C for grid cells south of the 47.5° parallel. We used the USA National Center for Atmospheric Research data for global monthly and annual precipitation (mm) and air temperature (°C) (LEGATES & WILLMOTT, 1990), interpolated to a 0.5° × 0.5° grid resolution.

For the analysis of species richness *versus* latitude all species occurring within the limits of a quadrat were included, even if their range only just extended to the respective quadrat.

Hot-spot definition

We initially defined as hotspots for reptiles and amphibians the top 10% among all 188 quadrats, ranked by the number of species they contain. This would give 19 quadrats. Since many quadrats have the same number of species, we made a small adjustment so that we selected 18 quadrats containing more than 25 reptile species and 17 quadrats containing more than 17 amphibian species.

Specifically for the checking of Rapoport's rule we excluded from the complete species list those species whose distribution range lies mainly outside the area under investigation. The Chameleon (*Chamaelo chamaeleon*) for example, is a species found at certain European localities (in the Iberian Peninsula and Greece) and in Asia Minor, but its main distribution range is in SW. Asia and N. Africa. This situation is found mainly in reptiles, not amphibians, and is due to the comparatively large number of asiatic reptile species present in the Caucasian region, Turkey and Greece. Species which have a comparatively wide distribution in Europe and also extend outside the area under investigation (such as *Chalchides chalchides*) have been included in the analysis. The species contained in the list of European herpetofauna but excluded from the analysis are listed in the Appendix).

According to the conventions of Rapoport's rule the important aspect of the geographic range of a species is its latitudinal range. We estimate the latitudinal range of a species as the difference between the maximum latitude of the northernmost quadrat and the minimum latitude of the southernmost quadrat in which the species occurs. An alternative measure of the degree of specialization of a species is the size of its distribution range calculated as the total number of quadrats in which it occurs. The latitudinal midpoint of a species (after COLWELL & HURTT, 1994) was estimated as the average latitude of the northernmost and southernmost quadrats of its range.

For the detection and clearer demonstration of areas that have species with a small range we did not apply a specific definition of "narrowness" for species range. Instead, we examined our data at three different levels of "narrowness". For amphibians we selected species that are found in up to 2, 6 and 10 quadrats whilst for reptiles we selected species found in up to 2, 5 and 10 quadrats. In this way, we could obtain a more realistic picture than if we had used one specific (and no less arbitrary) size of species range. At each level we calculated the total number of species meeting our criteria for each quadrat.

RESULTS

In the whole region a total of 129 reptile and 64 amphibian species have been recorded. The distribution of reptile and amphibian species richness in the area under examination is shown on figure 2a and 2b.

Reptiles present a monotonic decline in species number with increasing latitude (fig. 3a), (correlation coefficient $r = 0.82$ $P < 0.001$). At the top left of the graph there is a group of points which represent the quadrats of the Caucasian region. This region presents very high species numbers and is extremely rich in endemic reptile species. Amphibians appear to have a slight decline in species number at very low latitudes of the region and the peak in species richness is attained at mid latitudes, around 45° (correlation coefficient $r = -0.45$ $P < 0.001$). It should be noted, however, that this peak is partly the result of a wider spread of values at these latitudes.

Reptile richness is lower on the five out of the six islands that have been included in the study (the exception is Sicily) than in continental areas of the same latitude, whereas there is no such clear relationship for amphibians. This may happen because the range of values is wider than in reptiles, so that the relationship is obscured.

As a consequence of these species richness distribution patterns (fig. 2a and 2b), hotspot areas in the European region are identified as follows: the highest reptile species numbers are attained in the southernmost areas, while for amphibians there is a longitudinal variation in addition to a weak latitudinal gradient. The mid-latitude areas of western and central Europe are the richest areas for amphibian species.

The geographic range of species measured as the number of quadrats in which each species is found is very strongly correlated with species latitudinal range. The correlation coefficients are 0.92 for reptiles and 0.94 for amphibians. This indicates that latitudinal range and geographic range are equivalent as indices of the degree of specialization, at least in Europe.

The size of species range and their latitudinal midpoint is positively correlated (fig. 4). The correlation coefficients are 0.75 for reptiles and 0.80 for amphibians (both $P < 0.001$). The lower value of r for reptiles is due to a group of points at the lower end of the graph. Indeed, there are many species with a small range at middle latitudes (around 45° N). The great majority of these are the highly restricted endemic species

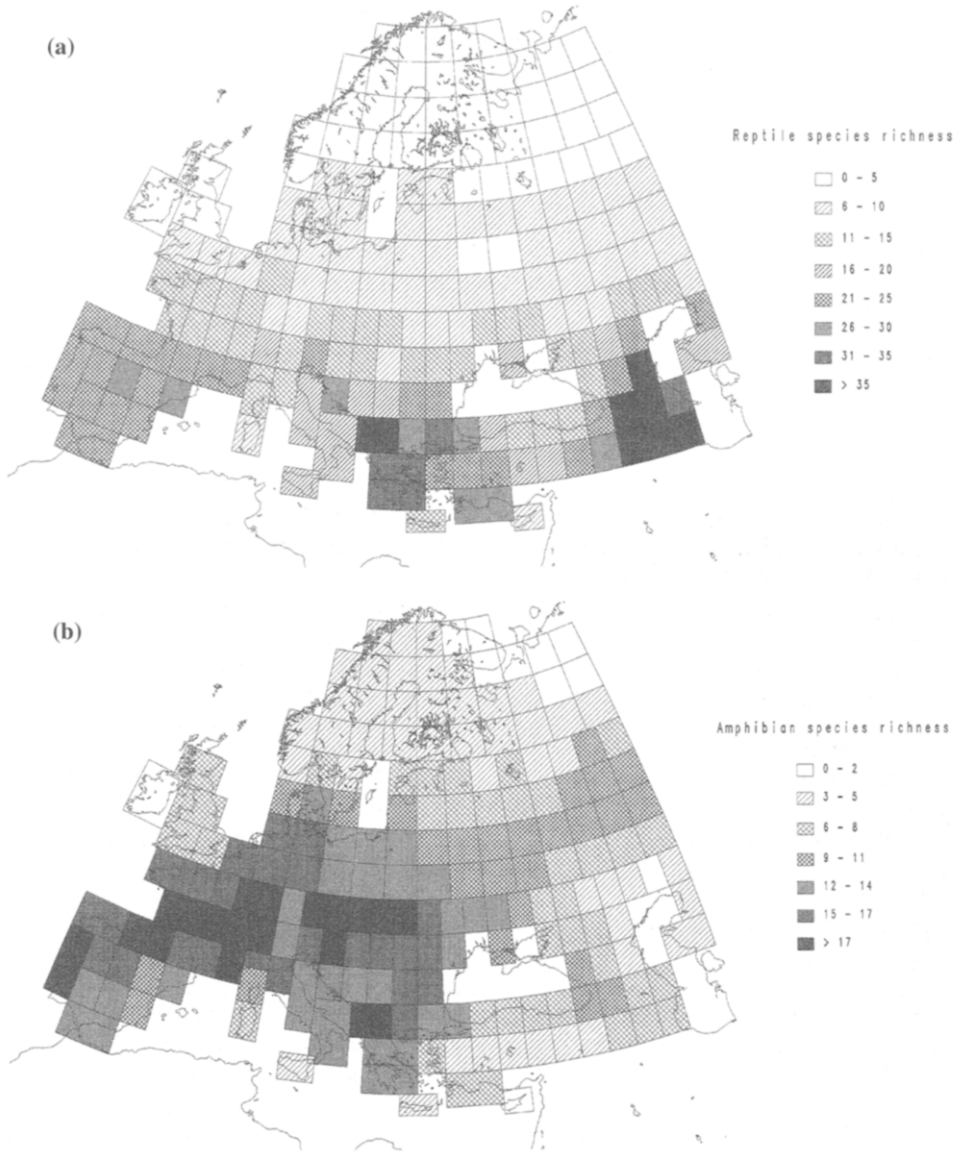


FIG. 2. – Distribution of herpetofauna richness in the western Palearctic, (a) Reptiles, (b) Amphibians.

of the Caucasian region. At high latitudes there are only widespread species *e.g.* the reptiles *Natrix natrix*, *Anguis fragilis*, *Lacerta vivipara*, *Vipera berus* and the amphibians *Bufo bufo*, *Rana ridibunda*, *Rana temporaria*, *Triturus cristatus*.

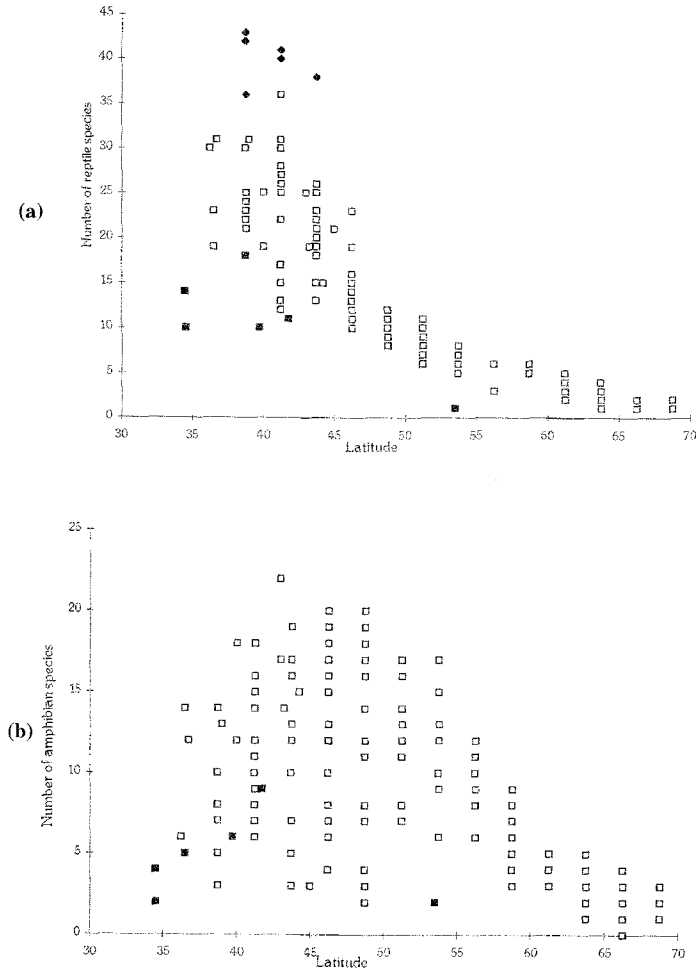


FIG. 3. — Relationship between latitude and species richness of (a) reptiles and (b) amphibians. The group of points at the top left of the graph 3a denoted by opaque diamonds, represents the quadrats of the Caucasian region. The group of points at the bottom left of the same graph denoted by opaque squares represents quadrats of islands that show decreased reptile species richness. Opaque squares in graph 3b, represent all the islands that have been included in the study.

Figures 5a, b, c and 6a, b, c show the distribution of species richness for small range reptile species which are found in only 2, 5 and 10 quadrats and for small range amphibian species that are found in 2, 6 and 10 quadrats respectively. For both taxa such species are clearly concentrated in the southern parts of the area.

The geographic variation of climatic descriptors is depicted on figure 7a, b. The correlation coefficients of the various descriptors of climatic variability with latitude

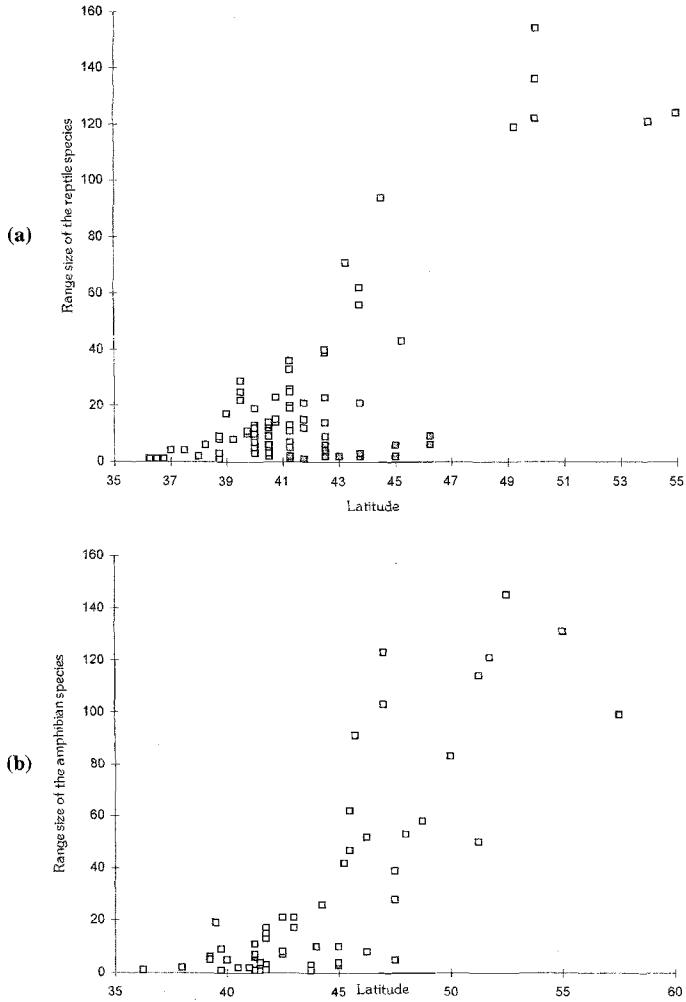


FIG. 4. – Relationship between the range size of (a) reptile species and (b) amphibian species and their range midpoints. In graph 4a, the group of points denoted by opaque squares represents the endemic species of the Caucasian region.

and species richness are presented in table I. Only annual temperature range increases slightly with latitude. It is evident though, from figure 7b and from the graphs of annual temperature range *versus* latitude (fig. 8a) and *versus* longitude (fig. 8b), that the annual temperature range is more connected with longitude than with latitude. All other climatic variability variables present a moderate to strong decline towards the north.

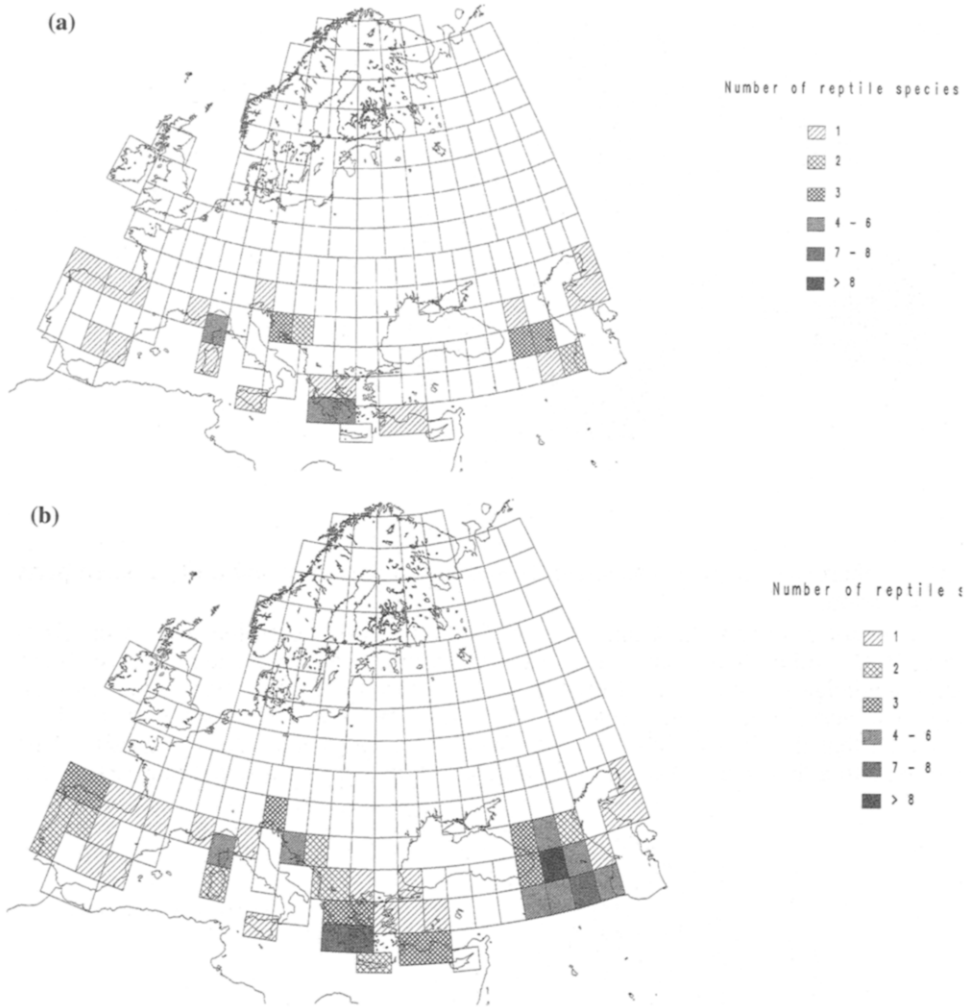


Fig. 5 (a), (b), (c). – Species richness maps of reptiles found in (a) up to 2 quadrats, (b) up to 5 quadrats and (c) up to 10 quadrats.

DISCUSSION

Our methodology for the estimation of species presence in a quadrat tends to overestimate the range of all species and especially of the highly restricted ones (endemics or ones with localized distribution). This method, however, is adequate in this case, taking into consideration the unequal distribution of sampling effort in the different parts of the area covered and the variation in data quality in the various sources used: available data are the product of intensive sampling in western Europe

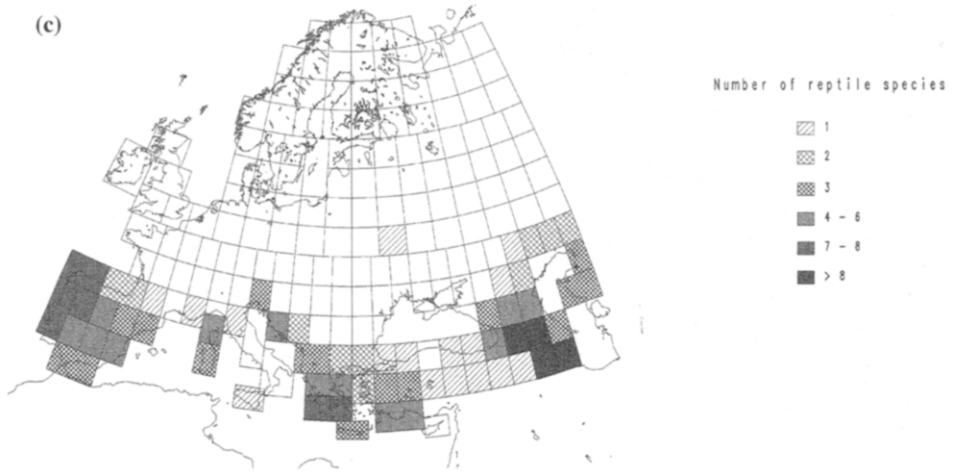


FIG. 5 (c).

whereas there are much less accurate data sources for eastern and north-eastern parts of the region.

It is not erroneous to assume that, with the possible exception of Britain (HARDING, 1991) and perhaps some other western European countries, the present status of our knowledge of species distribution may be considered as “satisfactory” only on large (or very large) spatial scales (GASTON, 1996). On such coarse scales, it is expected that the distributions of many species will appear to overlap greatly. This may lead to a false perception of coincidence of hotspots for different taxa (PRENDER-

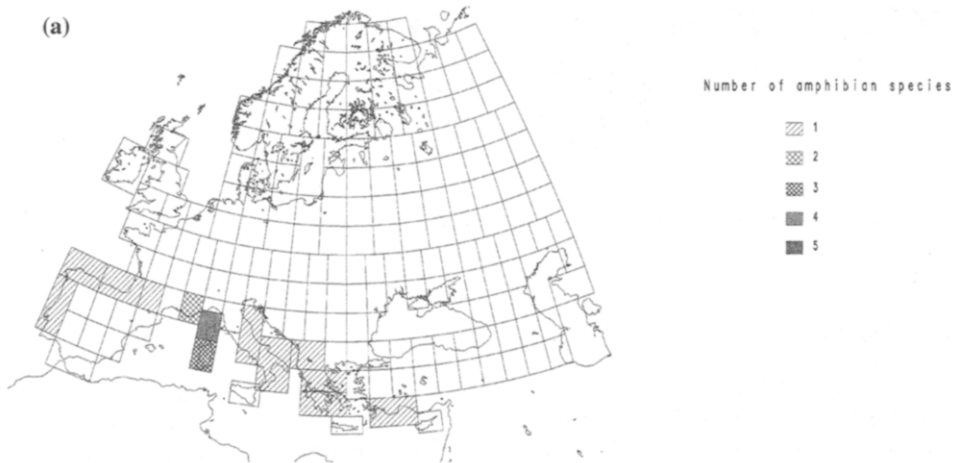


FIG. 6 (a), (b), (c). – Species richness maps of amphibians found in (a) up to 2 quadrats, (b) up to 6 quadrats and (c) up to 10 quadrats.

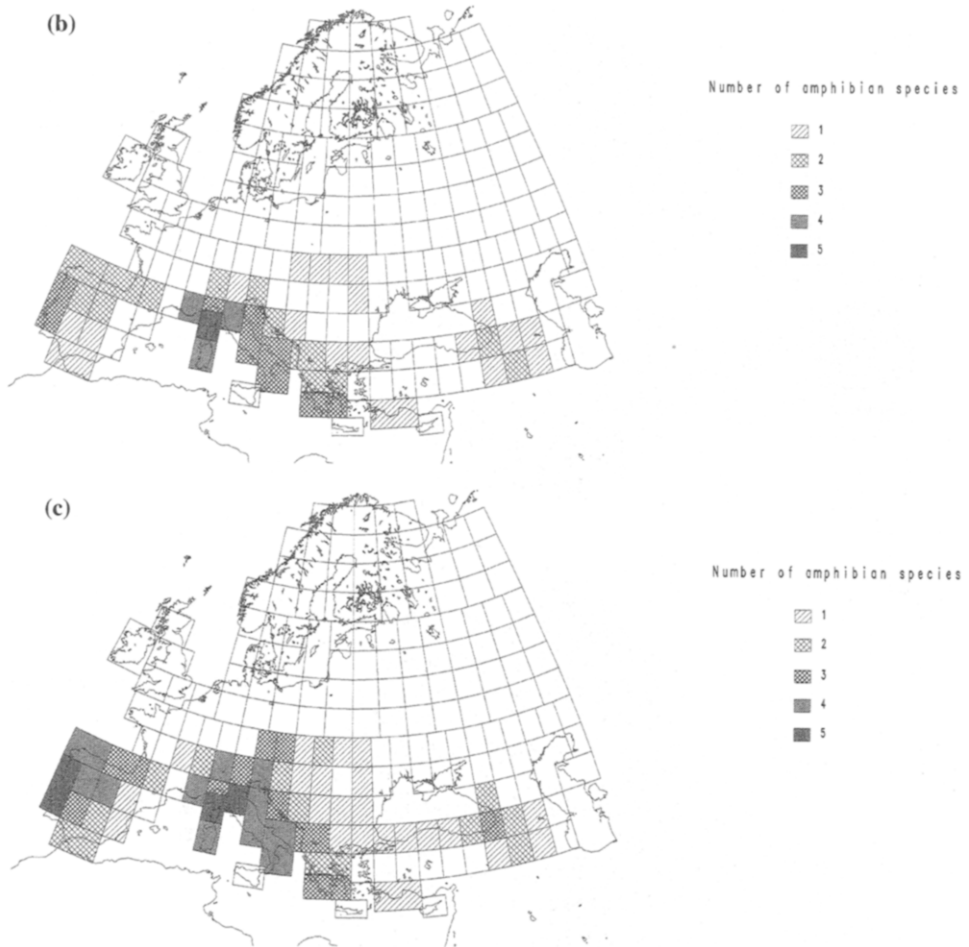


FIG. 6 (b), (c).

GAST *et al.*, 1993). Within his macroapproach of hotspots, MYERS (1990) has pointed out that the Mediterranean Basin (one among the 18 Earth's hotspot areas he defined) is so extensive that it can not rank in itself as a single hotspot area and that it would be necessary to identify key sectors that warrant special treatment. The perception of the coincidence of hotspots is not simply scale-dependent but essentially influenced by the interaction between spatial scale resolution and quality of species distribution data.

The distribution of species richness of the western palearctic herpetofauna follows a latitudinal gradient confirming the general trend of increasing species richness with declining latitude. These results are similar to those obtained for the N. American herpetofauna (CURRIE, 1991). Indeed, in both cases reptile species densities decrease

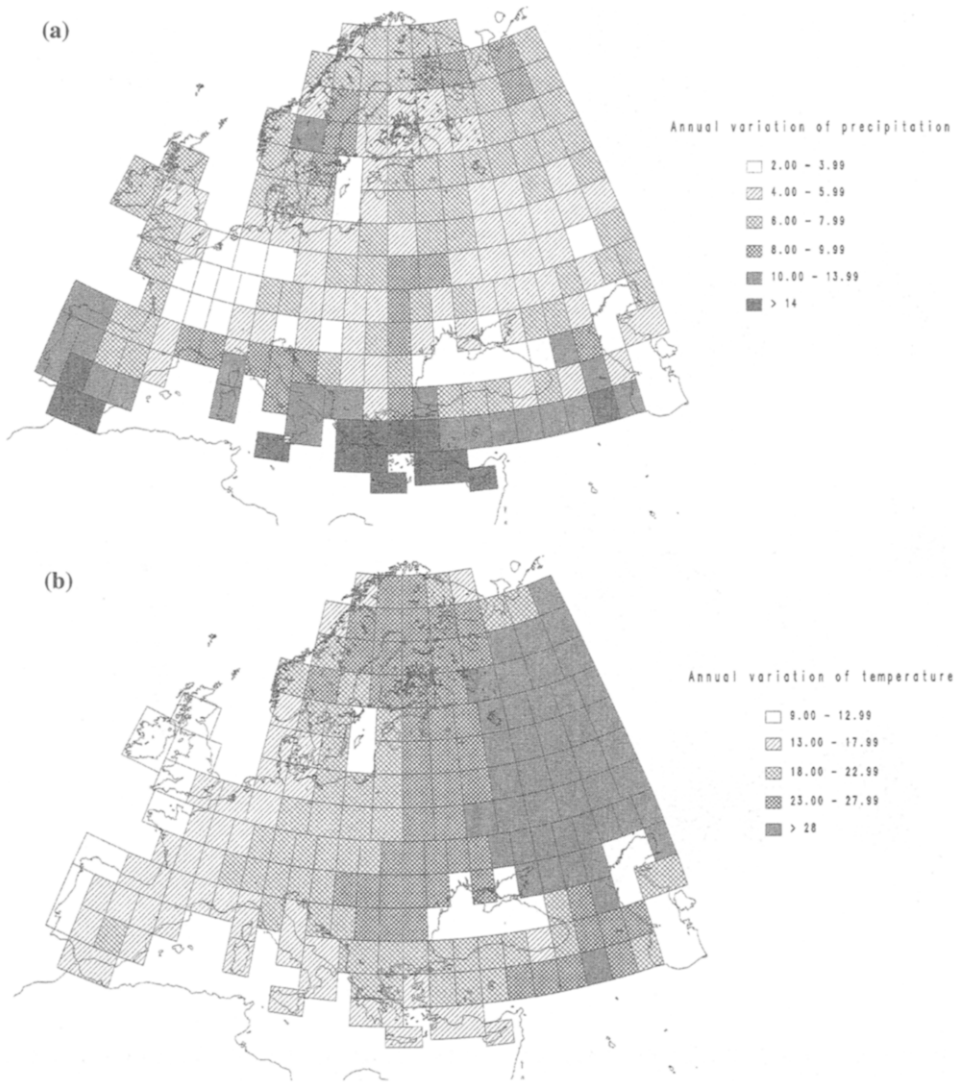


FIG. 7. – Geographical pattern of (a) precipitation variability and (b) temperature variability in the western Palearctic.

monotonically with latitude, while the correlation between latitude and amphibian species richness is not so strong. Amphibians show a mid-latitude peak in richness and a wide range of species richness values per quadrat. A remarkable situation arises from the high species richness and the great endemism in the Caucasian region. The islands we included in our study show that at least in the case of reptiles they contain smaller numbers of species compared to mainland areas of the same latitude.

TABLE 1. – Correlation coefficients between the variables used as indices of climatic variability, the latitude and the species richness (*, $P < 0.001$; **, $P < 0.005$; NS, not significant).

	Latitude	Reptiles	Amphibians
Precipitation variability for the whole year	-0.42*	0.41*	-0.2**
Precipitation variability for the active season of reptiles	-0.65*	0.48*	
Precipitation variability for the active season of amphibians	-0.63*		NS
Temperature variability for the whole year	0.3*	-0.21*	-0.4
Temperature variability for the active season of reptiles	-0.47*	0.24*	
Temperature variability for the active season of amphibians	-0.82*		0.19*

Reptiles and amphibians exhibit a different latitude-diversity relationship. The latitude gradient is a geographical gradient which generally represents corresponding ecological gradients, mainly ecosystem productivity. Thus, differences in patterns of reptile and amphibian diversity along the latitudinal gradient, in the studied region, should be examined within the general framework of the monotonic vs. unimodal “diversity-ecosystem function” gradient debate (see various treatments in RICKLEFS & SCHLUTER, 1993; HUSTON, 1994; ABRAMS, 1995). The unimodal or “hump-shaped” diversity-productivity curves are largely supported as the “true” (ROSENZWEIG, 1992) or the “ubiquitous” (HUSTON & DEANGELIS, 1994) pattern. According to this dominant theory, increased competitive exclusion at high productivity leads to decreased diversity. This assumption serves as the theoretical background for explaining worldwide patterns of diversity. Although challenged (ABRAMS, 1995), the dominant theory dismisses the monotonic increase pattern, independently of spatial scale.

In the case of the European herpetofauna, the fact that both types of relationships have been observed under the same data gathering protocol suggests that there is not obligatorily only one unique overall pattern of diversity response along ecological/geographical gradients, at least on a continental-wide basis. Unless the monotonic reptilian diversity increase is an artifact of the definition of the end-point of the latitudinal gradient in Europe (this corresponds to the hypothesis that if the latitudinal gradient was expandable geographically southward the diversity would decrease at lower latitudes), the explanation of the observed differences in the pattern should be related to taxonomic traits and ecology, and/or to species-area effects of specialized habitat requirements of amphibians and reptiles. Amphibians are a restricted taxonomic group which originates in wetlands, that is a particular habitat or environment. It is likely that amphibians would present their highest diversity in these types of environments in which they have spent most of their evolutionary history. Consequently, a non-monotonic pattern of diversity would obligatorily arise as a result of a non-uniform (or non-monotonic) geographic distribution of their required habitats. Amphibians which are not strictly related to wetlands are few in number and cosmopolitan, and they influence very little the overall pattern of this group.

Furthermore, the number of species found in a certain type of habitat increases with the areal extent of the habitat. We argue that the relative areal extent of a specific habitat required by a restricted taxonomic group along the latitudinal gradient may alone account for a diversity pattern. If wetland habitats are larger in total area in mid-latitude grid cells than in higher-latitude grid cells, this alone could account for the unimodal latitude-amphibian diversity pattern. The importance of correction for habitat size in studies of species diversity has been underlined by ROSENZWEIG &

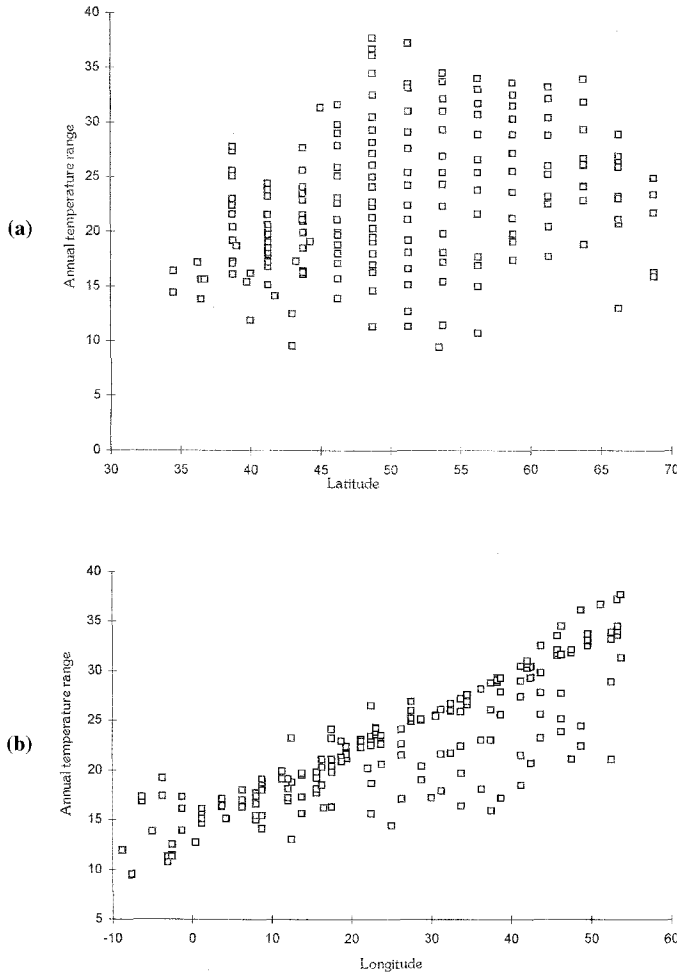


FIG. 8. – Relationships between the annual temperature range and (a) latitude ($r = 0.3, P < 0.001$), (b) longitude ($r = 0.85, P < 0.001$).

ABRAMSKY (1993) and ABRAMS (1995). These explanations of the unimodal diversity-latitude (see productivity) pattern for amphibians support the idea that this type of curve may be produced due to reasons independent of competition, contrary to what is supposed by the dominant theory.

Reptiles constitute a more ecologically diverse and less taxonomically restricted group of species spreading over a diversified range of habitats in comparison to amphibians. Consequently, the latitudinal pattern of diversity of reptiles would be less affected by the rarity of a particular habitat as seems to be the case with amphibians. The monotonic reptilian curve leads to a further support of the non-competition

related mechanisms accounting for diversity-latitude (see productivity) patterns. Undoubtedly, a diversity distribution pattern is generated by a combination of historical, abiotic, biotic and disturbance-related factors. The co-existence of both diversity patterns in the European herpetofauna suggests that, on a continental scale, competition is not the so-believed universal mechanism which determines the diversity-productivity pattern independently of taxonomic identity (and history) and ecology of species groups. Our results do not affirm the diversity-productivity theory (the unimodal pattern) and the competitive exclusion explanatory mechanism. They suggest that there are various alternative explanatory reasons accounting for the unimodal pattern, that the non-existence of these reasons may explain monotonic curves and that the universality of both unimodal pattern and mechanism is rather questionable.

The patterns for species richness obtained, show that the hotspot areas for the two taxa do not coincide (fig. 2). Hotspots for reptiles are the southernmost areas (Caucasian region, Greece and Iberia) while hotspots for amphibians are the western areas of middle latitude. Besides the geographic differentiation of the hotspots of the two taxa, there is a remarkable taxon difference in the percentage of the total number of species found in the hotspots areas: while the hotspots for reptiles contain 90% of the total number of the species recorded in the area, the corresponding percentage for the hotspots of amphibians is only 72%. This leads to the conclusion that for reptiles, the hotspots can be representative areas for the total fauna. On the contrary, the 28% of amphibian species found outside the hotspots, does not allow hotspots to be considered as clearly representative areas for the entire amphibian fauna in the region. For amphibians, species-rich areas are the result of the overlap of the ranges of widely distributed species.

Numerous hypotheses have been suggested to account for the latitudinal gradient in species richness (see reviews by PIANKA, 1966; RICKLEFS, 1990 and BEGON *et al.*, 1990). One of the suggested hypotheses is the "climatic variability hypothesis" according to which, as stated by BEGON *et al.* (1990), "(i) stable environments may be able to support specialized species that would be unlikely to persist where conditions or resources fluctuated dramatically, (ii) stable environments are more likely to be saturated with species and (iii) theoretical considerations suggest that a higher degree of niche overlap will be found in more stable environments". It is a hypothesis that has been given comparatively little attention, until reformulated by STEVENS (1989), who correlated it with the phenomenon he had called "Rapoport's rule". Through the formulation of this rule he drew our attention to another pattern which is the latitudinal gradient that exists in species distribution range. There is evidence that in many cases species range increases with latitude (for review see STEVENS, 1989), like for mammals in N. America (PAGEL *et al.*, 1991) and in the Palearctic (LETCHER & HARVEY, 1994).

This fact was attributed to the stability of the environment at lower latitudes which promotes the existence of specialized species (FRANCE, 1992). An individual organism near the poles experiences a wider range of climatic conditions than one at lower latitudes. In the former case selection pressure is against specialization: species are selected for a wide tolerance of climatic conditions, tend to be less restricted to a particular habitat type and consequently tend to be more widely distributed. Fewer generalist species can coexist per unit area than would be the case with specialist species because of competitive exclusion.

In conclusion, according to the above reasoning, species-rich areas or hotspots should be the result of the coexistence of many "specialized" species or species of narrow range. This fact constitutes one of the most important criteria for the confirmation of Rapoport's rule.

In figures 5 and 6, which show the distribution of European herpetofauna richness with respect to species geographic range, one can identify the areas that are rich in species of small range. By comparing these results with the maps of the distribution of herpetofauna richness in figure 2 we can clearly ascertain that for reptiles there is a clear coincidence between hotspots and areas rich in specialized species which means that the richness of these areas is due to the existence of many specialized or "narrow range" species. In the case of amphibians, the situation is very different. Amphibian species-rich areas are the central-western parts of Europe at about 45° N latitude. From the maps in figure 6, we see that the centres of the existence of species of small range are located in the southern regions of the continent which are not especially rich in species numbers. Moreover, by comparing figure 6 and the distribution of amphibian richness (fig. 2b), we can see that five quadrats out of 17 (30%) which are characterized as hotspots for amphibians, do not have a single species whose range is less than or equal to 10 quadrats, which is our criterion of "narrowness". Areas rich in amphibians contain species that are widespread in Europe. According to these results, Rapoport's rule holds for western Palearctic reptiles but not for amphibians.

Seasonal climatic variability as measured here does not increase with latitude in the European region. This finding is in contrast to the rule of seasonality increasing from the tropics to the poles. Although this rule is generally true on the global scale, on the continental scale the situation may be quite different. In the case of Europe, the southern Mediterranean part is characterized by climates of strong seasonal variation. Precipitation in particular is nearly always concentrated in the cold season – from autumn to spring – while the summers are very dry. The annual variation of temperature through Europe follows predominantly a longitudinal gradient rather than a latitudinal one (figs. 8a and 8b). This gradient is due to the effect of the ocean which gives a mildness to the climate of the western coastal parts of the continent.

Under these circumstances, in the European region, low seasonal variability does not seem to be connected with high species richness nor does it seem to promote the existence of small range reptiles and amphibians. LETCHER & HARVEY (1994) got similar results for the mammals of this region. The negative relations of climatic variability variables with range size which they found, made them express the view that the climatic variability variable may select for specialization rather than for a generalist lifestyle.

All of the above do not comply with the climatic variability hypothesis nor do they agree with the principle of competitive exclusion (which underlies this hypothesis) as the driving force for the determination of species richness.

In various studies that have been carried out the latitudinal gradient in species richness seems to be confirmed for most continents and for many taxonomic groups, except for Australia. Indeed as early as 1981, when PLANKA & SCHALL studied marsupial species, birds and various amphibian and reptile groups of Australia, they stated that "monotonically increasing latitudinal gradients in species densities towards the tropics, so celebrated in the literature are essentially non-existent in terrestrial vertebrates of Australia".

As in the case of the European herpetofauna, there is also a lack of coincidence of hotspots for various taxa in other continents (N. America and Australia). In N. America, hotspots for trees and amphibians are the SE coastal areas, while for mammals they are the SW coastal areas, and for reptiles the southern areas as is evident from the work of CURRIE & PAQUIN (1987) and CURRIE (1991). In Australia, hotspot areas for lizards are the dry central regions, whereas for avian groups and for amphibians, the most species rich areas are the wet coastal regions (SCHALL & PIANKA, 1978; PIANKA & SCHALL, 1981). For birds, the hotspots are found on the east coastal areas, for marsupials in eastern areas (SCHALL & PIANKA, 1978; PIANKA & SCHALL, 1981) and for mammals in general on the wet east coast and northern areas (SMITH *et al.*, 1994). The non-coincidence of hotspots confirms the view that each taxonomic group exhibits its own particular requirements on scales even as large as the continental scale.

In other cases in which the relationship between species range and latitude have been studied the results have been mostly similar to ours. Thus, for mammals in N. America (PAGEL *et al.*, 1991) and the Palearctic (LETCHER & HARVEY, 1994) there is a latitudinal gradient in the size of species range. However, the range size of Australian mammals increases towards the latitudinal centre of the continent and decreases towards the south (SMITH *et al.*, 1994). The patterns supporting Rapoport's rule in N. America and in the Palearctic are absent in Australia.

It was found that both in Australia (SMITH *et al.*, 1994) and in N. America (PAGEL *et al.*, 1991) the smallest ranges of mammalian species are found in areas of high topographic relief. The same pattern is evident for reptiles and amphibians in Europe. PAGEL *et al.* (*op. cit.*) and SMITH *et al.* (*op. cit.*) hypothesize that the range of species found in places of high topographic relief is delimited by mountains whilst in areas of low topographic relief the range of species is determined by the major climatic zones and consequently will be larger. This phenomenon cannot be attributed to a single mechanism. We can infer that the regions with many small-range species are either regions whence species cannot easily expand (*e.g.* due to physical barriers) or that they are refugia. In any case regions with many species of narrow range are regions with special geographic features (islands, mountains, peninsulas) that promote isolation.

The hypothesis of PAGEL *et al.* (*op. cit.*) and SMITH *et al.* (*op. cit.*) can be applied in the case of Europe: areas rich in reptile and amphibian species of narrow range do not necessarily coincide with hotspots and are located in the southern parts of the continent which are mountainous and fragmented. The morphology of the N. American continent which gets narrower and with higher topographic relief towards the south could also create the observed patterns in species range. Australia, on the contrary, presents a different morphology with an arid and flat centre and mountains in the south and in the east. This morphology renders Australia interesting as in this continent topographic relief does not decrease with latitude as happens in Europe and N. America. It would be interesting to investigate the range size of reptile species in Australia. If reptile species with a wide range are found in the flat and species-rich centre of this continent this would provide support for the hypothesis that species range is influenced more by topographic relief than by climatic variability. Wherever this is observed, an increase of average species range with latitude might well result from a concordant change in geographic complexity with latitude.

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APPENDIX

PALEARCTIC AMPHIBIANS WITH EXTRA-LIMITAL DISTRIBUTION

Discoglossus pictus
Hyla savignyi
Pleurodeles waltl
Salamandrella kayserlingii

PALEARCTIC REPTILES WITH EXTRA-LIMITAL DISTRIBUTION

Ablepharus kitaibelii
Agama ruderala
Agama sanguinolenta
Agama stelio
Alsophylax pipiens
Chalcides ocellatus
Chamaeleo chamaeleon
Coluber ravergieri (numifer)
Coluber rubriceps
Cyrtodactylus caspius
Cyrtodactylus russowi
Elaphe dione
Eremias arguta
Eremias velox
Eumeces schneideri
Gloydus halys
Lacerta saxicola
Lacerta stringata
Mabuya aurata
Macroprotodon cucullatus
Ophisaurus apodus
Ophisops elegans
Phrynocephalus mystaceus
Psammodromus algirus
Typhlops vermicularis
Vipera ursinii