

Influence of climatic gradients and colonization history on the present distribution of amphibians in the southern Po River basin (Italy)

Der Einfluß von Klimagradienten und Besiedlungsgeschichte auf die gegenwärtige Verteilung der Amphibien in der südlichen Po-Ebene (Italien)

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KURZFASSUNG

Die Herpetologische Datenbank des Naturhistorischen Museums von Ferrara beinhaltet 2355 Amphibiennachweise aus der südlichen Po-Ebene (Gebiet der Emilia-Romagna, 22124 km²). Die 16 darin registrierten Amphibientaxa gehören vier Chorotypen an, unter denen europäische Arten (31,2 %) über apenninische Endemismen und eurasische Arten (je 25 %) sowie über italische Endemismen (18,8 %) dominieren.

Anhand dieser Nachweise wurde das Verbreitungsmuster der Amphibienformen der Po-Ebene durch eine Clusteranalyse veranschaulicht. Diese stellt die Zusammensetzung der Amphibienformen in 69 UTM Rasterquadraten von 20 km x 20 km Größe mit Hilfe von Jaccards Ähnlichkeitskoeffizienten dar. Das Dendrogramm zeigt zwei Hauptverbreitungsgruppen, die einerseits dem höhergelegenen Teil der Apenninen, andererseits der Po-Ebene samt den Vorbergen des Apennins entsprechen. Die Zuordnung der Arten mit Hilfe des Multi-Dimensional Scaling Verfahrens ergab ein ähnliches Bild, sodaß zwei Gruppen von Taxa festgelegt werden konnten sowie die Arten, die jede der beiden Zonen charakterisieren. Die beobachtete Aufteilung folgt einem Höhengradienten und dementsprechend auch einem pluviometrischen Gradienten, welche die Verbreitung der Amphibien in der Po-Ebene beeinflussen und auch gut erklären.

Die Apenninen sind insbesondere durch vergleichsweise niedrigere Temperaturen und höhere Niederschläge und damit die Ausbildung eines montanen Klimagürtels ausgezeichnet, der durch Buchenwälder, *Vaccinium*-Heiden und in größerer Höhen durch Grasland charakterisiert ist. Drei Arten sind innerhalb des Untersuchungsgebietes für diese Zone exklusiv: *Rana temporaria*, *Salamandra salamandra*, und der Apenninen-Endemit *Speleomantes strinatii*. Im Gegensatz dazu sind die Vorberge der Apenninen sowie die Po-Ebene durch vergleichsweise höhere Temperaturen und geringere Niederschläge charakterisiert wie sie für den submediterranen Vegetationsgürtel typisch sind. In dieser Zone ist der Norditalische Endemit *Rana latastei* für die Po-Ebene exklusiv.

Die obengenannten Unterschiede zeigten sich auch in der Häufigkeitsverteilung der chorologischen Kategorien: Apenninen-Endemiten und europäische Chorotypen waren in den Gebirgsgegenden häufiger, italische Endemiten und eurasische Chorotypen herrschten im Gebiet der Po-Ebene vor.

ABSTRACT

The Herpetological Data Base of the Natural History Museum of Ferrara contains 2,355 amphibian records of the southern Po River basin (Emilia-Romagna region, 22,124 km²). The 16 amphibian taxa involved represent four chorotypes, in which European species (31.2 %) prevail over Apennine endemisms, and Eurasian species (25 % each) and Italian endemisms (18.8 %).

Based on the above records, the distribution pattern of the amphibian taxa in the southern Po River basin was visualized by a cluster analysis which classified the amphibian composition of the 69 UTM 20 km x 20 km squares constituting the sampling stations on the basis of Jaccard's similarity coefficient. The dendrogram obtained showed two main distributional groups corresponding to the higher part of the Apennines Mountains and to the southern Po River plain plus Apennine foothills. Ordination of the species by Multi-Dimensional Scaling resulted in a similar pattern, so that two groups of taxa were determined as well as the species characterising each zone. This partitioning observed was paralleled and well explained by an altitudinal and consequently thermo-pluviometric gradient influencing the distribution of the amphibians in the southern Po River basin.

The Apennines are characterized in particular by comparatively lower temperatures and higher rainfall; this determines a montane bioclimatic belt, characterized by beech woods, *Vaccinium* heaths and grasslands at high altitudes. Three species are exclusive to this zone within in the study area: *Rana temporaria*, *Salamandra salamandra*, and the Apennine endemic *Speleomantes strinatii*. In contrast, the Apennine foothills and Po plain zone is characterized by comparatively higher temperatures and lower rainfall, as is typical to sub-Mediterranean vegetation belts. In this zone the North Italian endemic *Rana latastei* is exclusive to the Po River plain.

The above differences were also shown by the distribution of the frequencies of chorological categories: Apennine endemics and European chorotypes were more frequent in the mountainous area, whereas Italian endemics and Eurasian chorotypes prevailed in the Po plain zone.

KEY WORDS

Amphibia; thermometric and pluviometric gradients, species distribution, chorology, eco-biogeography, southern Po River basin, Italy

INTRODUCTION

Even on a systematic level, the distribution patterns of poikilothermic vertebrates are influenced by climatic factors (DARLINGTON 1957; OWEN 1989; POUGH et al. 1998), temperature and precipitation in particular. Spatial gradients in richness and diversity of amphibian species have been studied by several authors (ROGERS 1976; SHALL & PIANCA 1977; ANTUNEZ et al. 1988; MANN et al. 1991; WOJNARSKI & GAMBOLD 1992; REAL et al. 1993; HECNAR & M'CLOSKEY 1996). Many factors involving thermo-pluviometric, altitudinal, latitudinal and vegetation features have been identified to explain these gradients. The influence of these climatic and environmental parameters on the distribution range of amphibian species has been related to the biogeographic origin of amphibian chorotypes (BURY & PEARL 1999).

Italy is among the European countries with the highest numbers of amphibian species and endemic amphibians (DUELLMAN 1999). The amphibian fauna of the southern Po River basin in northern Italy, recently investigated by MAZZOTTI (1992), MAZZOTTI & STAGNI (1993) and MAZZOTTI et al. (1999) is characterized by species of Eurasian and European origin, but most of all by the high number of Italic endemisms due to the presence of species originating from ancient stocks of the Tertiary which remained isolated, and to a more recent speciation in the Quaternary (BOLOGNA & MAZZOTTI, in press).

This study represents an eco-biogeographical analysis which correlates local distribution patterns of amphibians with thermo-pluviometric and altitudinal data.

STUDY AREA AND METHODS

The study area corresponds to the Emilia-Romagna Region, 22,124 km² in size, situated between 43°44' - 45°08' N and 09°12' - 12°45' E, and bordered by the Po River in the North, the Apennines mountain ranges in the South and West and the Adriatic Sea in the East. This area can be subdivided roughly into two geographic zones: mountainous areas, with a mean altitude of 1,000 m, and plains plus coast (fig. 1). The climate can be described by a thermo-pluviometric gradient in which mean annual temperatures tend to drop by 0,6 °C in altitudinal steps of 100 m from the plain towards the mountains, while mean annual rainfall increases by approximately 50 mm (SERVIZIO METEOROLOGICO REGIONALE 1995).

In the Apennines, this climatic gradient determines a phytoclimatic habitat differentiation into three vegetation belts: 1) montane, composed of beech woods and *Vaccinium* heaths; 2) cool sub-Mediterranean, composed of *Ostrya-Aceretum*, with *Sorbus aria*, *Calamagrostis varia* and *Aremonia agrimonoides*; 3) warm sub-Mediterranean *Ruscus aculeatus* and *Pyracantha coccinea*. In the plain area, the Adriatic coastal zone

can be distinguished from the inland Po River plain zone (UBALDI et al. 1996). On the Adriatic coast there is a small residual portion of pine-woods and holm-oak woods (PICCOLI et al. 1983; CORBETTA et al. 1984). In the Po River plain intense anthropic activity has produced a strongly reduced differentiation of habitats; in fact, the wild vegetation cover has almost completely been replaced by agricultural plantations there.

This study is based on a total of 2,355 amphibian records made from 1980 to 1998 and stored in the Herpetological Data Base of the Natural History Museum of Ferrara (MAZZOTTI et al. 1999). We treated *Rana lessonae* CAMERANO, 1882 and *R. kl. esculenta* LINNAEUS, 1758 and potential other water frogs as one taxon, since they were taxonomically and ecologically indistinguishable to us during the survey. *Pelobates fuscus insubricus* CORNALIA, 1873 was not included in the study, as only recently some individuals were seen at coastal stations of the study area (MAZZOTTI & RIZZATI 2001; MAZZOTTI et al. 2003).

Each record includes locality, altitude, coordinates within its 10 km x 10 km UTM grid, habitat type and information about the

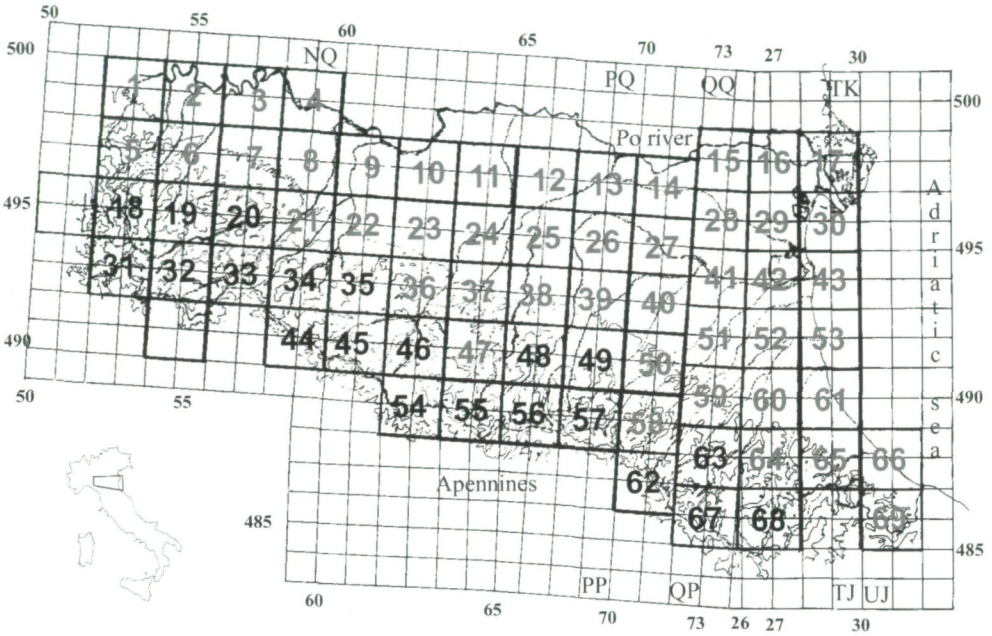


Fig. 1: Map of the study area (southern Po River basin, northern Italy) including 10 km x 10 km UTM squares grid system overlay. The 69 territorial units (20 km x 20 km UTM grid squares) used for amphibian distribution pattern analysis are framed by bold outlines and numbered consecutively. Their zonal assignment as obtained by cluster analysis (fig. 2) is indicated as follows:
 Grey numbering – grid squares assigned to the Po plain zone;
 black numbering – grid squares assigned to the Apennine zone.

Abb. 1: Karte des Untersuchungsgebietes (südliche Po-Ebene, Norditalien) mit dem Gitternetz des 10 km x 10 km UTM-Rasters. Die 69 zur Untersuchung der Verbreitungsmuster herangezogenen Gebietseinheiten (20 km x 20 km UTM-Raster) sind fett umrandet und fortlaufend numeriert.
 Ihre zonale Zuordnung durch die Clusteranalyse (Abb. 2) ist wie folgt gekennzeichnet:
 Graue Numerierung – der Zone "Po-Ebene" zugeordnete Rasterflächen;
 schwarze Numerierung – der Zone "Apenninen" zugeordnete Rasterflächen.

specimens observed (MAZZOTTI et al. 1999). In order to assess the distribution patterns of the amphibian species, the study area was divided into 69 U.T.M. squares of 20 km x 20 km each (fig. 1). A cluster analysis was performed on a presence/absence matrix, classifying the 69 squares of the grid with Jaccard's similarity coefficient (JACCARD 1908); after double square root transformation of the data, UPGMA was the linkage method used (SNEATH & SOKAL 1973). The ordination of the amphibian species was performed based on their presence / absence in each of the UTM squares according to multi-dimensional scaling (MDS) (KRUSKAL 1964).

The amphibian species were assigned to chorological categories according to LA GRECA (1943, 1962) and VIGNA TAGLIANTI et al. (1993), however modified. In fact regarding the amphibians we distinguished two categories of the Italic chorotype: Italic endemism and Apennine endemism (table 1).

The climate data of the region were collected from 61 thermo-pluviometric and 90 pluviometric climate sampling stations between 1951 and 1994 (SERVIZIO METEOROLOGICO REGIONALE 1995). These data were used to calculate, for each territorial unit, the mean temperatures, the highest temperature value of the warmest month and the lowest temperature value of the coldest

Table 1: The amphibians of the southern Po River basin (northern Italy) assigned to chorological categories. For the two zones Apennine (Ap – 21 UTM squares) and Po River basin (Po – 48 UTM squares), the number of 20 km x 20 km UTM squares holding records is indicated.

Tab. 1: Die Amphibien der südlichen Po-Ebene (Norditalien) und ihre Zuordnung zu chorologischen Kategorien. Die Anzahl der 20 km x 20 km UTM-Rasterquadrate mit Nachweisen ist jeweils für die Zonen Apenninen (Ap – 21 UTM-Rasterquadrate) und Po (Po – 48-UTM-Rasterquadrate) angegeben.

Taxon	Ap	Po	Chorotype
			Eurasian (25%)
<i>Triturus vulgaris</i> (LINNAEUS, 1758)	20	41	Centralasian-European-Mediterranean
<i>Bufo bufo</i> (LINNAEUS, 1758)	21	47	Centralasian-European-Mediterranean
<i>Bufo viridis</i> LAURENTI, 1768	2	45	Asian-European-Mediterranean
<i>Rana temporaria</i> LINNAEUS, 1758	12	0	Centralasian-European
			European (31.2 %)
<i>Salamandra salamandra</i> (LINNAEUS, 1758)	19	0	European
<i>Triturus alpestris</i> (LAURENTI, 1768)	18	5	Centraleuropean
<i>Triturus carnifex</i> (LAURENTI, 1768)	21	43	S-European
<i>Rana lessonae</i> CAMERANO, 1882	20	46	European
+ <i>R. kl. esculenta</i> LINNAEUS, 1758			
<i>Rana dalmatina</i> BONAPARTE, 1840	16	36	European
			Apennine endemisms (25 %)
<i>Salamandrina terdigitata</i> (LACÉPÈDE, 1788)	6	3	Apennine
<i>Speleomantes italicus</i> DUNN, 1923	9	6	Apennine
<i>Speleomantes strinatii</i> (AELLEN, 1958)	3	0	Apennine
<i>Rana italica</i> DUBOIS, 1987	17	6	Apennine
			Italic endemisms (18.8 %)
<i>Bombina pachypus</i> (BONAPARTE, 1838)	11	8	Apennine and Sicily
<i>Hyla intermedia</i> BOULENGER, 1882	10	43	Italic and Sicily
<i>Rana latastei</i> BOULENGER, 1879	0	7	N-Italic

month, the mean annual rainfall and the thermo-pluviometric index of EMBERGER (see UBALDI et al. 1996):

$$I_E = 2000 * P / (M^2 - m^2)$$

where P is the mean annual rainfall (mm); M is the mean highest temperature value (°K) of the warmest month; m is the mean lowest temperature value (°K) of the coldest month.

RESULTS

Geographical zone and climatic gradients

The cluster analysis which classified the 20 km x 20 km squares revealed two main groups: one corresponding to the Apennine mountains and the other to the Po River plain including its coastal zones and the belt of the foothills of the Apennines (fig. 2). The former group is composed of 21 UTM squares, in which there is a mean of 9.5 species per square at a mean altitude of 808.6 m a.s.l. (SD = 352.6). The latter group includes 48 UTM squares, an average of 6.7 species per square and a mean altitude of 120.2 m a.s.l. (SD = 172.4). Map figure 1

illustrates this subdivision. In the Apennine mountainous zone annual rainfall is, on the average, 1214.5 mm (SD = 240.9), while in the Po River plain zone the average is 717.4 mm (SD = 111.8) ($t = 71.8, df = 67, p < 0.01$). Mean annual temperature is 10.3°C (SD = 1.7) in the mountainous zone, and 12.3°C in the plains (SD = 0.7) ($t = 99.1, df = 67, p < 0.01$). In the Apennine mountainous zone, the mean value of Emberger's index is 157.0 (SD = 65.3), while in the Po River plain area mean I_E is 85.6 (SD = 15.7) ($t = 61.0, df = 67, p < 0.01$). Hence, the differences between the Apennine mountainous and the Po River plain zones are significant in all three above parameters.

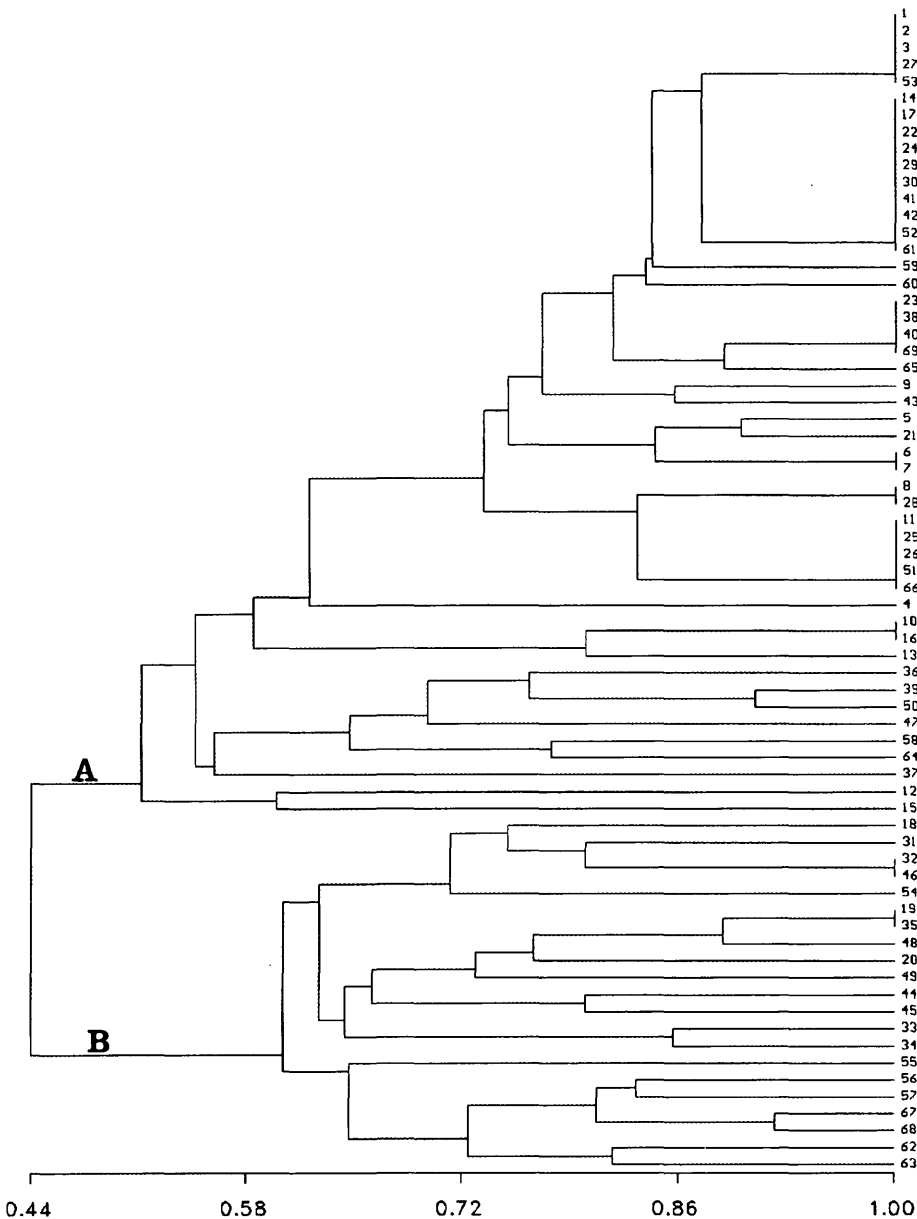


Fig. 2: Dendrogram classifying the 69 UTM 20 km x 20 km grid squares studied according to similarities in their amphibian species composition. The two groups corresponding to Po plain and Apennine zones are marked by A and B. Numbering of the cases on the right refers to the numbering of the UTM grid squares in figure 1.

Abb. 2: Dendrogramm zur Darstellung der Ähnlichkeiten in der Zusammensetzung der Amphibienfauna bei den 69 untersuchten 20 km x 20 km UTM-Rasterfeldern. Die beiden Gruppen, die den Zonen "südliche Po-Ebene" und "Apenninen" entsprechen sind mit A und B gekennzeichnet. Die Fallnummerierung rechts bezieht sich auf die Numerierung der UTM-Rasterfelder in Abbildung 1.

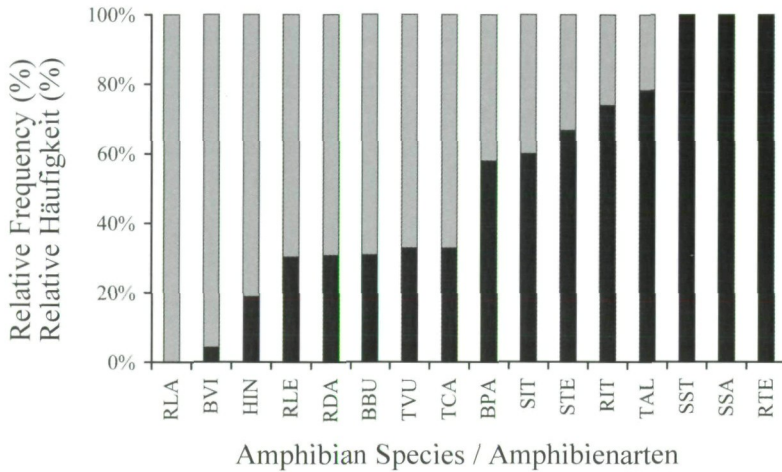


Fig. 3: Relative frequency (%) of amphibian records in the Po River Plain (gray) and Apennine Mountains zones (black). Percentage frequencies were calculated according to the number of 20 km x 20 km squares occupied in the respective geographical zones out of the total number of squares in which the species was observed.

Abb. 3: Relative Häufigkeit (%) der Amphibiennachweise in den Zonen "Po-Ebene" (grau) und "Apenninen" (schwarz). Die prozentuellen Häufigkeiten ergeben sich aus dem Anteil der in der jeweiligen geographischen Zone belegten 20 km x 20 km Rasterfelder an der Gesamtzahl der Rasterfelder, in denen die Art beobachtet wurde.

BBU - *Bufo bufo*, BPA - *Bombina pachypus*, BVI - *Bufo viridis*, HIN - *Hyla intermedia*, RDA - *Rana dalmatina*, RLE - *Rana lessonae/esculenta*, RIT - *Rana italica*, RLA - *Rana latastei*, RTE - *Rana temporaria*, SIT - *Speleomantes italicus*, SSA - *Salamandra salamandra*, SST - *Speleomantes strinatii*, STE - *Salamandrina terdigitata*, TAL - *Triturus alpestris*, TCA - *Triturus carnifex*, TVU - *Triturus vulgaris*.

Amphibian distribution patterns

Sixteen amphibian species (7 Caudata and 9 Anura – water frogs treated as one taxon, see table 1) were found, that is to say, 25.7% on the total of 66 European and 47.2% on the total of 36 Italian amphibian species (SOCIETAS HERPETOLOGICA ITALICA 1996; GASC et al. 1997). On the average, each species was recorded in 147 localities, with a maximum of 367 records in *Bufo bufo* (LINNAEUS, 1758) and a minimum of 11 in *Rana latastei* BOULENGER, 1879, and an average of 2.2 records per UTM square (10 km x 10 km). The study did not include *Rana catesbeiana* SHAW, 1802, a species introduced from North America and naturalized in the Po plain (MAZZOTTI & STAGNI 1993).

Analysis of the records of amphibian species in the two geographical zones revealed a wide spectrum of frequencies and distribution patterns reaching from exclusive species, such as *Rana temporaria* LINNAEUS, 1758, *Salamandra salamandra*

(LINNAEUS, 1758) and *Speleomantes strinatii* (AELLEN, 1958) in the Apennines and *R. latastei* in the Po zone, to species sporadic in the montane and frequent in the plain zone such as *Bufo viridis* LAURENTI, 1768 and vice versa such as *Rana italica* DUBOIS, 1987, *Triturus alpestris* (LAURENTI, 1768) and *Salamandrina terdigitata* (LACÉPÈDE, 1788) (table 1, fig. 3). Percentage frequencies were calculated according to the number of 20 km x 20 km squares occupied in the respective geographical zones out of the total number of squares in which the species was observed.

The species associations outlined by MDS ordination, tended to reproduce the distribution patterns already highlighted by the territorial subdivision (fig. 4). In fact the MDS ordination showed the species ubiquitous and characteristic of the Po plain on the right, and the species characteristic of the Apennines on the left. *Rana latastei* and *Sp. strinatii* are very confined in their actual distribution and rare; this could explain

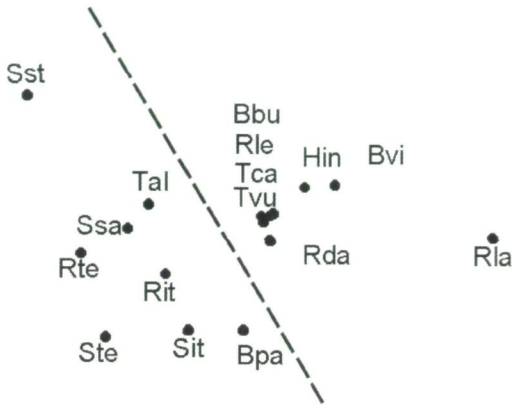


Fig. 4: Ordination of the amphibian species by multi-dimensional scaling (MDS), stress of configuration = 0.11. For species codes see fig. 3.

Abb. 4: Anordnung der Amphibienarten auf Grundlage von multi-dimensional scaling (MDS), Stresswert = 0,11. Abkürzungen für die Arten siehe Abbildung 3.

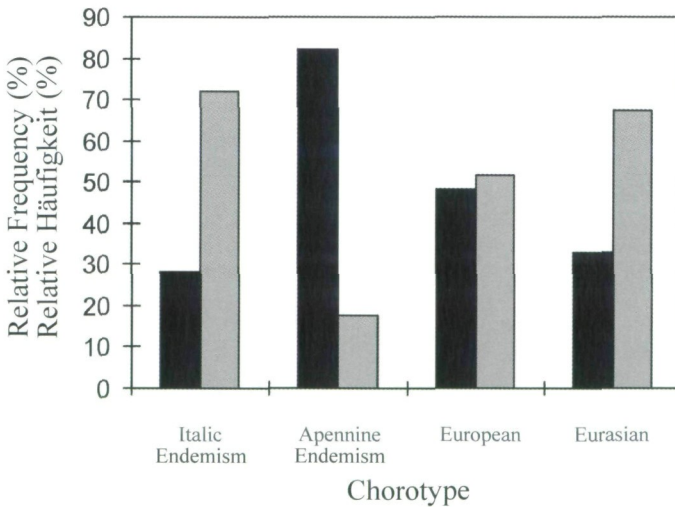


Fig. 5: Relative frequency (%) of the records of amphibians of the Po plain (gray) and Apennine (black) zones in each chorological category (chorotype).

Abb. 5: Relative Häufigkeit (%) der Nachweise von Amphibien der Zonen "Po-Ebene" (grau) und "Apenninen" (schwarz) in jeder der chorologischen Kategorien (Chorotypen).

their particular allocation relative to the two main groups in the plot.

The chorological categories involved formed four groups of chorotypes (table 1),

of which the European was the richest (5 species, 31.2 %) followed by both Eurasian chorotype and Apennine endemism (4 species, 25.0 % each) and, finally, the Italic

endemism (3 species, 18.8 %). The frequency distribution of chorotypes revealed a marked distinction between the Apennine and Po plain regions (fig. 5). The montane

area is characterized by Apennine endemisms and European species, while the Po plain area is distinguished most of all by Italic endemisms and Eurasian species.

DISCUSSION

The ordination of the 20 km x 20 km squares shows two main groups of amphibians: the first one corresponds to the Apennines and the second to the Po plain (fig. 1). This distribution is paralleled by an altitudinal and thermo-pluviometric gradient. The Apennines are characterized by lower temperatures and higher rainfall; this area contains three exclusive species: *R. temporaria*, *S. salamandra*, and the Apennine endemism *Sp. strinatii*. On the contrary, the Po plain is characterized by higher temperatures and lower rainfall; exclusive to this area is the North Italic endemism *R. latastei* (fig. 3). This difference is also shown by the distribution of the frequencies of chorological categories, in that Apennine endemisms and European chorotypes are more frequent in the mountain area, whereas Italic endemisms and Eurasian chorotypes are the most frequent species in the Po plain (fig. 5).

This distribution can be explained by the chorological origin of the amphibian species of the study area. Eurasian and European chorotypes are characterized by widespread species within the western Palaearctic region. These species spread from parts of Eastern Europe and Asia towards Western Europe, particularly during the cold periods of the Pleistocene characterized by a cool steppe climate at the lowest altitudes and even colder temperatures in the mountains, and thus, spatially overlapped with the remaining species of the former thermophilic fauna (LA GRECA 1962). During this process, some species entered the Italian Peninsula through a land bridge which – for a certain period – emerged from the Adriatic Sea to link the Balkans and the Italian Peninsula and then underwent speciation in Italy with respect to the eastern vicariant species. An example for this is *R. italica* which differentiated from *Rana graeca* BOULENGER, 1891 (PICA-

RIELLO et al. 1990, 1996; MENSI et al. 1992). Other species probably occupied the northern Mediterranean areas during the Pleistocene reduction of their Middle European range, like *S. salamandra*, *Rana dalmatina* BONAPARTE, 1840 and *Triturus vulgaris* (LINNAEUS, 1758) (BOLOGNA & MAZZOTTI in press). In the below taxa separation may have been more recent and differentiation may be less pronounced, e.g., *R. latastei* (see CAPULA et al. 1991), *Triturus carnifex* (LAURENTI, 1768) (see BUCCINNOCENTI et al. 1983; RAFINSCHI & ARNTZEN 1987; WALLIS & ARNTZEN 1989) and *Hyla intermedia* BOULENGER, 1882 (see NASCETTI et al. 1995) or *Bombina pachypus* (BONAPARTE, 1838), isolated in the Italian Apennine and in vicariance with *B. variegata* (LINNAEUS, 1758) (NASCETTI et al. 1982). After their southward dispersion during the coldest diluvial periods, some populations of the most widespread European and Eurasian species remained isolated in the Apennine area: among them *Triturus alpestris apuanus* (BONAPARTE, 1839) and the Apennine populations of *R. temporaria* (LANZA 1965; CAPULA & BAGNOLI 1982; GROSSENBACHER 1997; ZUIDERWIJK 1997; DENOËL et al. 2001). In the Apennines two endemic Italic genera are found: *Speleomantes* is the only Palaearctic genus of the lungless salamanders of the family Plethodontidae, and the current coexistence of two Apennine species – *S. italicus* DUNN, 1923 and *S. strinatii* – is the result of the isolation of an ancient Oligocene or Miocene stock in the south-western part of Europe, formerly widespread in the Palaearctic area (NASCETTI et al. 1996; FORTI et al. 1998); *Salamandrina* is an Italian monotypic and endemic genus, very ancient too, and currently present only in the Apennines with the specie *S. terdigitata* (BARBIERI 2001).

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