

# A tribute to Hubert Saint Girons: niche separation between *Vipera aspis* and *V. berus* on the basis of distribution models

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**Abstract.** Interspecific competition in contact areas is a major topic in ecological studies. A number of studies were carried out on European vipers, focusing on contact areas between two or three species characterized as appropriate by ecological needs more or less similar. The aim of this study is to extend the analysis of this topic to the case of *Vipera aspis* and *V. berus* in an alpine area of northern Italy, by comparing suitability models to verify which ecological factors affect their occurrence and to assess a possible niche separation. Potential distribution was modelled using the maximum entropy method, using six non-correlated ecogeographical variables as predictors. The models fitted well for both species (mean AUC = 0.926; 87.4% of testing data correctly classified). The most informative variables were: habitat, altitude and solar radiation for the asp viper; altitude and habitat for the adder. Deciduous woods, meadows and urban areas had a positive effect on *V. aspis* distribution as wetlands, meadows and rocks vegetation did on *V. berus*. However, the variable best separating the species was the elevation, the adder occurring more frequently at higher altitude than the asp viper. Our data showed that the two vipers were mutually exclusive, as already observed by Saint Girons in 1975. *Vipera aspis* is more thermophilic and lives at low altitude, while *Vipera berus* lives under cool and humid areas typical of alpine pastures. A similar pattern were found in the contact areas between European vipers belonging to the *V. aspis* and *Pelias* group respectively.

**Keywords:** distribution, maximum entropy model, niche separation, *Vipera aspis*, *Vipera berus*.

## Introduction

The use of geostatistical analyses supported by GIS (Geographic Information System) to infer distribution patterns of animal species became more and more important in zoological studies during the last decades and many models were developed to predict habitat suitability (Hirzel et al., 2006; Traill and Bigalke, 2006; Tsoar et al., 2007; Ortega-Huerta and Townsend Peterson, 2008). These techniques were also used in herpetology and, in particular, many studies used predictive modelling techniques to shape species distribution for biogeographical and conservation purposes (Santos et al., 2006; Pearson et al., 2007; Bombi et al., 2009; Sillero and Tarroso, 2010). In addition, many papers attempting to preview future distribution

of declining and invasive species were also published, often based on climatic data series (Ficetola, Thuiller and Miaud, 2007; Pyron, Burbrink and Guiher, 2008; Rödder et al., 2008; Ficetola, Thuiller and Padoa-Schioppa, 2009; Sillero, 2009, 2010).

Geostatistical models could also be used to analyse distribution relationships among different species to verify if they are sympatric, parapatric or allopatric, but it would be more interesting the use of these mathematical methods to ascertain if different species live under similar ecological conditions. In this case, some considerations about niche overlap or separation could be done, but only a few papers dealt with this topic in herpetological research (Brito and Crespo, 2002; Martínez-Freiría et al., 2008).

Niche separation is a major topic in ecological research and it is a result of the competition when two or more species with similar ecological requirements share the same geographic area (Pianka, 1993; Martínez-Freiría et al., 2010). Natural selection is expected to promote a separation among coexisting species in order to minimize interspecific competition. Niche compe-

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tion occurs on three main dimensions: food, space and time (Pianka, 1993).

In reptiles niche overlapping has been previously studied in lizards (Carretero and Llorente, 1993; Pérez-Mellado et al., 1993) and snakes (Luiselli and Rugiero, 1991; Luiselli, 2006; Metzger, Ursenbacher and Christe, 2009). However niche competition study is particularly interesting when species belonging to the same genus live in sympatry, because they may share feeding habits and habitat features. In addition, closely related species share similar ecological habits because they are recent descendents of a common ancestor, thus they are likely to compete when a contact area occurs after a long separation; in this scenario, they are a good model to test interspecific competition and ecological niche conservation after species separation (Wiens and Graham, 2005).

European vipers are a monophyletic group (Lenk et al., 2001) including species with similar ecological niches; species are mostly parapatric, but in some cases pairs of species have some contact zones where competition could occur (Luiselli, 2006; Martínez-Freiría et al., 2010). Contact areas have been recorded for example for *Vipera aspis/V. berus* (Saint Girons, 1975; Monney, 1996), *V. seoanei/V. latastei* (Brito and Crespo, 2002), *V. aspis/V. ursinii* (Luiselli et al., 2007), *V. aspis/V. latastei* (Martínez-Freiría et al., 2010); a unique case of an overlap area among three species occurs in Northern Spain for *V. aspis/V. latastei/V. seoanei* (Martínez-Freiría et al., 2008). A pioneeristic research about vipers competition was conducted by Saint Girons (1975) in northern France on *V. aspis* and *V. berus*. These species share a narrow area in the Loire-Atlantique region, partitioning microhabitats and using different reproductive strategies (Saint Girons, 1975). Habitat partitioning was confirmed also by Monney (1996) in Switzerland.

The asp viper and the adder occur in apparent sympatry in many areas of central and east-

ern Italian Alps, but no study about their coexistence has been published until now.

Since 2000 we are carrying out a long term study on vipers distribution in central Alps in order to investigate the relationships between species distribution and both habitat features and human presence. In this paper we analyse the relative distributions of the asp viper and of the adder in a contact area of central Alps using a maximum entropy model to highlight ecological factors affecting their occurrence and to ascertain if a niche separation can be hypothesised.

## Materials and methods

### Study area

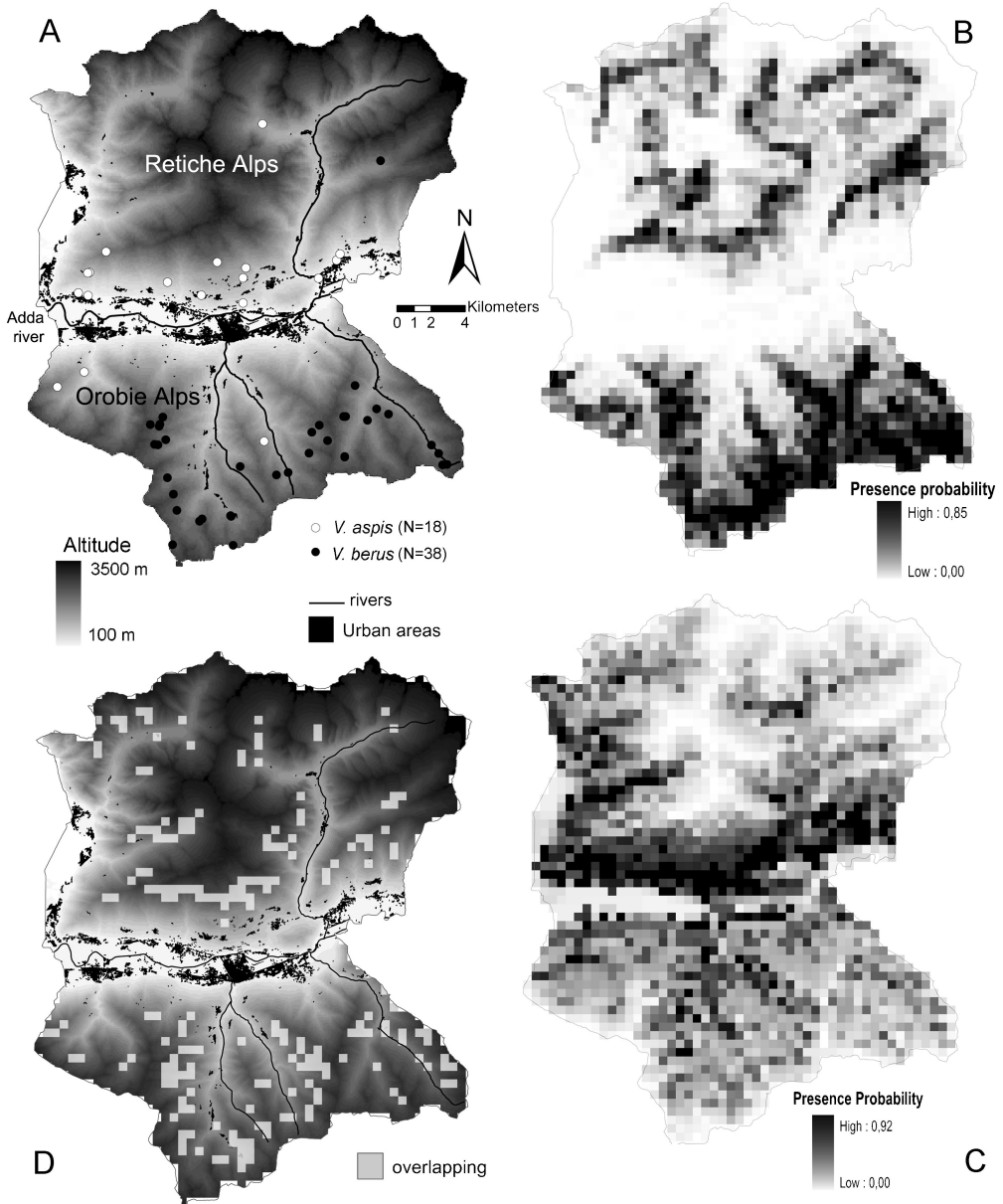
The study area is the central portion of Valtellina (Northern Italy), the greatest valley of Lombardy (46°10.3'N; 9°34.2'E). It is West-East oriented and it is characterized by two main mountain sides: the Retiche Alps and the Orobie Alps. The former is South exposed, while the latter is North exposed and they are separated by the Adda river in the valley bottom. The area extends over 585 km<sup>2</sup> and ranges from 200 to 3600 m a.s.l. Climate is hybrid between temperate and cold (respectively *Cfb* and *Dfb* in the Köppen system), without a dry season and with a warm summer (Peel, Finlayson and McMahon, 2007). In this scenario, the Retiche Alps are continental while the Orobie Alps are mainly temperate.

### Species occurrence data

From 2000 and 2006 systematic visual encounter surveys were performed across the study area, by transects covering all main habitats types and altitudes. The transects were uniformly distributed all over the study area, in order to obtain a dataset reflecting actual distribution of the two vipers (Elith et al., 2011). Fifty-nine records (*Vipera aspis*  $n = 19$ ; *V. berus*  $n = 40$ ) were collected. Each viper was recognised and its geographical location was recorded using a GPS. The so-obtained occurrence data were then resampled to a 500 meters grid reducing respectively to 18 and to 38 the presence sites for *V. aspis* and for *V. berus* (fig. 1A).

### Ecogeographical data

Three kinds of ecogeographical variables (EGVs) were considered (table 1), which accounted for the study area (i) climate (19 variables), (ii) geomorphology (altitude and slope), and (iii) environment (habitat type and solar radiation intensity). All the 23 EGVs were resampled to a 500 meters grid so that each cell had a single value for each variable. We preliminarily checked for multicollinearity among



**Figure 1.** Map of the study area including data records (A). Presence probability map for *V. berus* (B) and *V. aspis* (C). Overlapping cells at prevalence threshold (D).

EGVs by examining cross-correlations matrix (Pearson and Spearman correlation coefficients) among them, based on 250 sample points (the 59 presence records plus 191 random points). Then we considered for the subsequent analyses only the EGVs that satisfied the following two conditions: (i) no correlation coefficient exceeding 0.75, and (ii) only one representative variable from a set of highly correlated EGVs ( $r \geq 0.75$ ; Martínez-Freiría et al., 2008; Kumar and Stohlgren, 2009). In this way only six EGVs (table 2) were considered for spatial analyses.

#### Modelling procedure

The distributions of the two species were modelled using the maximum entropy method (carried out by the software Maxent 3.3.3, <http://www.cs.princeton.edu/~schapire/maxent/>), which performs well even with small samples and bases on presence-only data (Elith et al., 2006; Hernandez et al., 2006; Pearson et al., 2007; Tsoar et al., 2007; Ortega-Huerta and Townsend Peterson, 2008). Maxent is a machine learning approach that estimates the distribution of a species

**Table 1.** Source and range of variation for the six EGVs finally considered in building the models.

EGVs	Type	Range	Source
Altitude	Continuous	100-3200 m	Contours <a href="http://www.cartografia.regione.lombardia.it/geoportale/ptk">http://www.cartografia.regione.lombardia.it/geoportale/ptk</a>
Habitat	Categorical	17 categories	DUSAF 2007 <a href="http://www.cartografia.regione.lombardia.it/geoportale/ptk">http://www.cartografia.regione.lombardia.it/geoportale/ptk</a>
Slope	Continuous	0°-65°	Derived from contours
Solar radiation	Continuous	2-22 MJ/m <sup>2</sup> ·d	Derived from contours using SOLARFLUX ( <a href="http://www.wsl.ch/staff/niklaus.zimmermann/programs/aml1_8.html">http://www.wsl.ch/staff/niklaus.zimmermann/programs/aml1_8.html</a> ; Dubayah and Rich, 1995).
Annual precipitation	Continuous	1030-1831 mm	<a href="http://www.worldclim.org">www.worldclim.org</a> ; Hijmans et al. (2005)
Precipitation seasonality	Continuous	12%-34%	See <a href="http://www.worldclim.org">worldclim.org</a> for details

**Table 2.** Pearson or Spearman (\*) correlation coefficients for the six used EGVs.

	Solar radiation	Habitat	Altitude	Slope	Annual precipitation
Habitat	0.12*				
Altitude	0.04	0.45*			
Slope	-0.17	-0.18*	0.13		
Annual precipitation	0.22	0.36*	0.71	0.04	
Precipitation seasonality	-0.20	-0.39*	-0.46	0.17	-0.72

by finding the probability distribution of maximum entropy (i.e., closest to uniform) subject to constraints represented by the known information about the species distribution itself. These constraints are formalized by imposing that the expected value of each EGV must be close to its average over presence sites (Phillips, Anderson and Schapire, 2006; Phillips and Dudík, 2008; Elith et al., 2011). The software evaluates an exponential function of the EGVs which assigns a probability value (called “raw” value) to each point used to build the model (presence sites plus background pseudo-absent points); then it projects these raw values to the whole study area. This projection represents the model output, but raw values suffer from two kinds of problems: (i) they are difficult to interpret at locations not used during model training because they do not represent a presence probability; (ii) they are scale-dependent, that is they depend on the number of background points used, because all raw values must sum to one (Phillips, Anderson and Schapire, 2006). By the 3.3.1 release, these problems have been solved by converting the primary exponential model into a logistic one, so that projected values were scale independent and may be easily interpreted as probability of presence (Phillips and Dudík, 2008).

Models building followed the same steps for both species and made use of a bootstrap procedure for validation. First, the original set of occurrence point was randomly divided into a training sample (80% of the observations) and a test sample (20%): the training sample was used to build the model and the test sample to validate it. The same procedure was repeated ten times for each species using different training and testing samples and producing ten distribution models for each original dataset. The average

of the ten replicates was used as a synthetic model and it was employed in the subsequent analysis (Araújo and New, 2007; Pearson et al., 2007).

Model performance was estimated in two ways: the first one was the percentage of correctly classified testing data. As this procedure requires a probability threshold value to discriminate between presence and absence, prevalence (i.e., the proportion of species occurrences among all the sites) was chosen (Liu et al., 2005). The second one was the mean AUC (Area Under Curve) of training data. AUC is the area under the Receiver Operating Characteristics (ROC) curve, and it is a measure of the ability of the model to discriminate between absence and presence sites (Bradley, 1997; Fielding and Bell, 1997; Fawcett, 2006). The AUC value is 0.5 for the uniform distribution and it rises to 1 for a perfect model built using presence/absence data. With presence-only data, this upper limit is difficult to estimate, but, in any case, it is less than 1 (Wiley et al., 2003). However, the higher the value is, the better the model fits. Values above 0.75 indicate a potentially useful model (Elith, 2002).

The contribution of each EGV to the model was evaluated with a jackknife analysis of the average regularized gain. The gain represents how much better the model fits the data than the uniform distribution does. For each EGV two models were computed: one with only that variable (“only-with” model), and one with all the remains (“without” model). The most important variables are expected to significantly reduce the gain of the “without” model with respect to the comprehensive model (with all the EGVs) and to produce a relative high gain for the “with-only” model (Phillips, Dudík and Schapire, 2004). An heuristic

estimate of average percentage contribution of each variable to the full model was also used (see Phillips, Anderson and Schapire, 2006 for details).

The response curve generated by Maxent for each EGV was used to visually investigate the relationship between each ecogeographical variable and the presence probability of the vipers. To avoid the effect of interaction with other variables, these curves were derived by the model built with only one variable at a time (Phillips, Anderson and Schapire, 2006).

#### Niche overlap

The extent of niche overlap between *Vipera aspis* and *V. berus* was measured by Schoener's *D* (Schoener, 1968) and the metric *I*, developed by Warren et al. (2008, 2010). Both statistics quantify predicted niche similarity by a direct comparison of the probabilities assigned to each cell by the two models. The indices range from 0 (no overlap) to 1 (complete overlap), and were computed by ENMTools (<http://enmtools.blogspot.com/>). An identity test (Warren et al., 2008; Leaché et al., 2009; Pyron and Burbrink, 2009; Costa and Schlupp, 2010) was carried out to establish niche equivalence: the observed values of *D* and *I* were compared with a distribution of values of *D* and *I* based on 100 randomized pseudoreplicates. Each pseudoreplicate was obtained by: (i) pooling the data of the two species, (ii) randomly extracting two new samples with the same sizes of the original ones, (iii) generating a distribution

model for each one of the datasets, (iv) and computing niche similarity indices (*D* and *I*) between these two new models. In this way a distribution of *D* and *I* values was obtained under the null hypothesis of niche equivalence and it could be used to assess significance of the observed values (Warren et al., 2010).

## Results

The distribution model for *Vipera aspis* was obtained averaging ten replicates and the mean AUC was  $0.917 \pm 0.037$  (table 3; fig. 1C). Using prevalence as the threshold to discriminate between presence and absence, the percentage of correctly classified testing localities was 83.3% and the proportion of suitable sites was 34.5% of the study area. The most important EGVs, ordered by percentage of contribution, were habitat, solar radiation and altitude (table 4). These variables showed the highest gain values in the individual EGV models, and they caused the greatest "gain loss" if removed from the full model. The analysis of the re-

**Table 3.** Models summary. Regularized training gain, area under ROC curve (AUC), and prevalence were reported both for training and testing sample.

	Species	
	<i>Vipera aspis</i>	<i>V. berus</i>
Training sample	15	31
Test sample	3	7
N. of replicates	10	10
Model gain	$1.275 \pm 0.468$	$1.240 \pm 0.197$
Training AUC	$0.917 \pm 0.037$	$0.935 \pm 0.016$
Test AUC	$0.891 \pm 0.052$	$0.897 \pm 0.041$
Prevalence	$0.153 \pm 0.070$	$0.144 \pm 0.027$
Test omission at prevalence threshold	83.33%	91.43%
Suitable area at prevalence threshold (%)	34.5%	32.3%

**Table 4.** EGVs importance. For each EGV were reported: the gain value without the variable, the gain with only the variable and the estimated percentage of contribution.

EGVs	Training gain without the EGV		Training gain with only the EGV		Percentage contribution	
	<i>V. aspis</i>	<i>V. berus</i>	<i>V. aspis</i>	<i>V. berus</i>	<i>V. aspis</i>	<i>V. berus</i>
	Altitude	$1.18 \pm 0.47$	$0.77 \pm 0.14$	$0.41 \pm 0.17$	$0.70 \pm 0.10$	$16.7 \pm 8.9$
Habitat	$0.83 \pm 0.28$	$1.08 \pm 0.17$	$0.71 \pm 0.38$	$0.43 \pm 0.10$	$51.9 \pm 16.7$	$23.2 \pm 9.1$
Solar radiation	$1.06 \pm 0.44$	$1.22 \pm 0.20$	$0.26 \pm 0.13$	$0.05 \pm 0.04$	$20.5 \pm 11.9$	$2.2 \pm 1.8$
Slope	$1.19 \pm 0.46$	$1.11 \pm 0.23$	$0.06 \pm 0.03$	$0.15 \pm 0.09$	$7.6 \pm 3.7$	$12.4 \pm 8.5$
Annual precipitation	$1.25 \pm 0.46$	$1.13 \pm 0.14$	$0.16 \pm 0.04$	$0.14 \pm 0.07$	$1.3 \pm 1.5$	$10.4 \pm 5.8$
Precipitation seasonality	$1.25 \pm 0.46$	$1.22 \pm 0.19$	$0.06 \pm 0.04$	$0.17 \pm 0.08$	$2.0 \pm 2.0$	$4.1 \pm 4.4$

sponse curves for these three factors pointed out (fig. 2): (i) the positive effect of the urban areas, the deciduous woods and the meadows on presence probability; (ii) the increase in presence probability with the rising of solar radiation; (iii) the negative effect of altitude, which maximized presence probability between 100 and 1100 m a.s.l., and reduced it to less than 0.1 above 2100 m.

The mean AUC for *V. berus* models was  $0.935 \pm 0.016$  (table 3, fig. 1B) and 91.4% of the testing localities were correctly classified. The suitable area at prevalence threshold was 32.3% and the most informative EGVs were: altitude and habitat, while the other variables had a relative small contribution (table 4). The response curves for these two main factors showed (fig. 2): (i) the positive role played by meadows, high altitude wetlands, shrubs and conifers woods on presence probability; (ii) the “Gaussian” shape of altitude response, which exhibited a presence probability higher than 0.5 between 1600 and 2000 m a.s.l.

The measured *D* and *I* indexes of niche overlap were respectively 0.627 and 0.888. Both this values were significantly lower ( $P < 0.01$ ; 100 pseudoreplicates; mean  $D = 0.777 \pm 0.043$ ; mean  $I = 0.953 \pm 0.017$ ) than expected under the null hypothesis of niche identity. So, each of the two vipers had its own ecological niche.

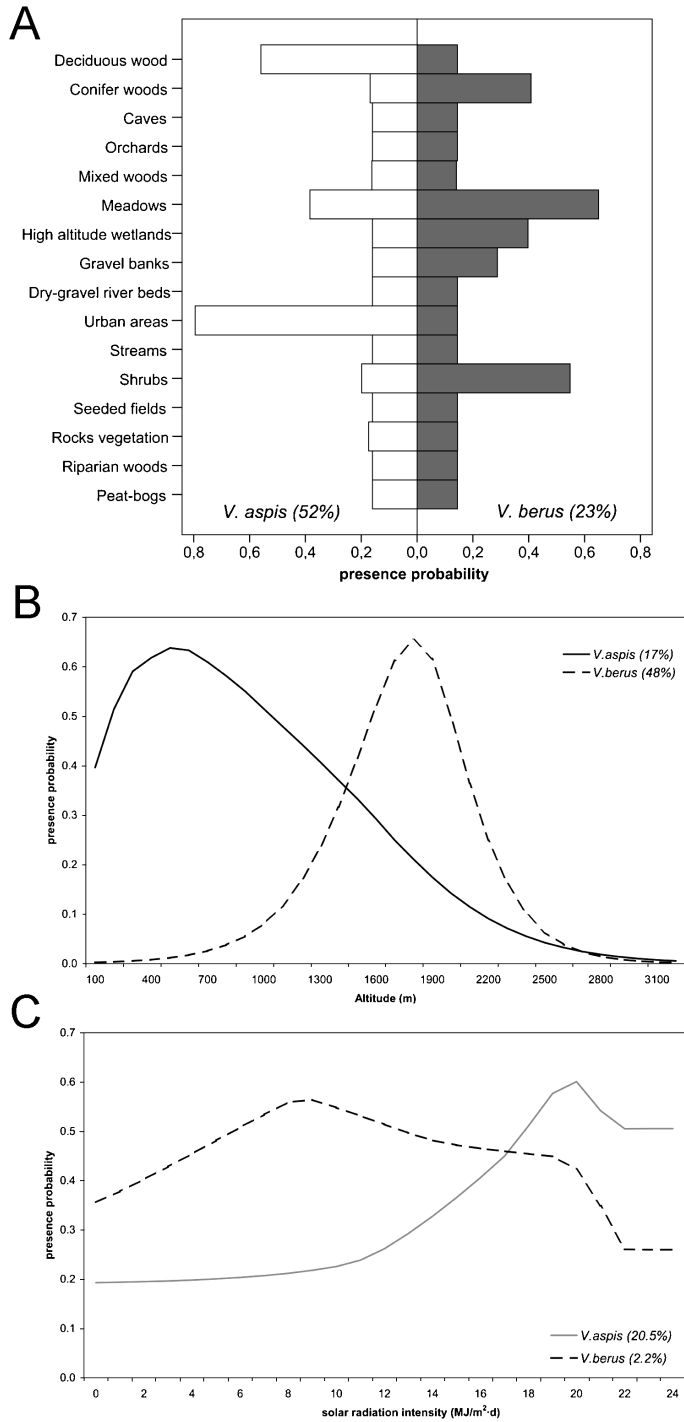
Using prevalence as the absence/presence threshold, the percentage of overlapping area was 8.4% of the whole study area (fig. 1D). It corresponded respectively to the 24.3% of suitable cells for *V. aspis*, and to the 26.0% for *V. berus*. These values were comparable to those obtained looking at the proportion of occurrence points which fell into overlapping cells: 22.2% for the asp viper and 31.6% for the adder. However, the mean probability values for these cells was higher for *V. berus* (0.39) than for *V. aspis* (0.24). So these areas seemed to be more suitable for the adder, even though there was not an observed prevalence of *V. berus*. To better

understand this apparent incongruity, a map resulting from the product of the two models was computed (fig. 3), in order to estimate the co-occurrence probability. This map showed that none of the cell had a probability higher than 0.50 (max value: 0.28) and only 3 cells (0.13%) exceeded 0.25. Therefore the high probability value for *V. berus* could partially be a bias due to the threshold approach.

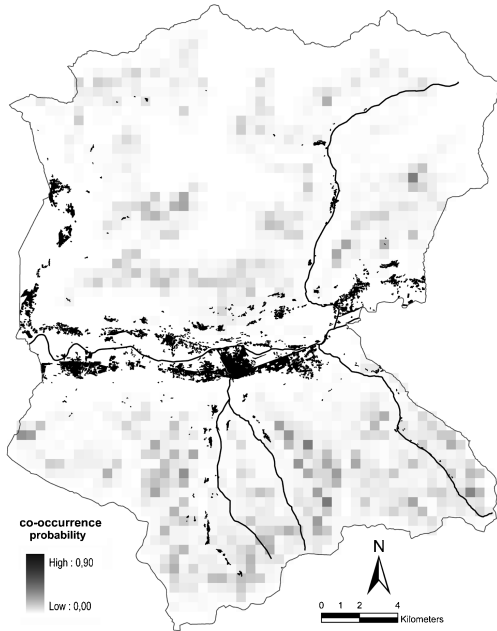
## Discussion

*Vipera aspis* and *V. berus* partially overlapped in the study area (8.4% of shared suitable cells), nevertheless they maintained distinct ecological niches, as assessed by the identity test. The overlap was limited to the highest part of the study area (900-2200 m), which appeared to be more suitable for *V. berus* than for *V. aspis*, even though the proportion of observed presence sites were similar for the two species. This apparent inconsistency could be the consequence of the sample bias associated to the threshold approach and/or to the difficulties in exploring mountainous zones, suggesting that a research focused on the area of overlap might be helpful to validate the ecological models. Anyway, the environmental conditions of the shared zones appeared quite unsuitable for *V. aspis* and this issue could act as a limiting factor avoiding contact between the two species. Consequently, in the contact zone, *V. berus* might be able to use also the habitat of the asp viper, but the opposite was not likely. Very similar results have been previously reported by Monney (1996) in Switzerland, even though at a much lower spatial scale. In view of all above, the two species appear to be simply juxtaposed and competition between them is probably prevented because they could not really interact.

In this scenario, the relative distribution at a small scale appeared almost parapatric, with a clear separation on an altitudinal gradient: the asp viper had a maximum of probable occurrence at 500 m a.s.l., whereas the adder had a peak at about 1800 m a.s.l. Altitude was the



**Figure 2.** Response curves for the most important eco-geographical variables for both species: habitat (A), altitude (B), and solar radiation (C). Probability values were averaged among the ten models.



**Figure 3.** Map of the probability of co-occurrence of *V. aspis* and *V. berus*. It was obtained as the product of the two model.

most important factor explaining habitat suitability for *V. berus* and it accounted for 47.6% of the model, whereas it accounted for 16.7% for *V. aspis*. Altitude is related to a temperature gradient, which is probably the key factor explaining the relative distributions of the two species, because the asp viper is a thermophilic species (Saint Girons, 1975; Mallow, Luiselli and Rugiero, 1990; Ludwig and Nilson, 2003), as emphasized by the importance of solar radiation in the species distribution model (20.5%). On the contrary, the adder lives under cold and humid climates that allow its presence even in northern latitudes (Saint Girons, 1975; Mallow, Ludwig and Nilson, 2003).

Habitat was an important variable for both species (51.9% for *V. aspis* and 23.2% for *V. berus*): in particular, meadows played a major role for the two vipers, but the asp viper was related also with deciduous woods and urban areas, whereas the adder more probably occurred in high altitude wetlands, shrubs, and rocks vegetation. Habitat preferences for these species were studied by many authors and *V. aspis* pres-

ence is usually related to open, sunny and arid areas, with deciduous vegetation offering natural refuges and ecotones (Mallow, Ludwig and Nilson, 2003). Hardly wooded areas were not suitable for this species, because thermoregulation is more difficult, particularly in Alpine high altitude sites, where climate is less favourable, as demonstrated in other zones, where abandoned meadows were replaced by woods in a few years (Jäggi and Baur, 1999). Suitable areas for the adder in the Alps are usually high altitude meadows and wetlands, with abundant shrubs (e.g., rhododendrons, blueberries), and outcropping rocks.

Some hypotheses could explain the high positive effect of urban areas on asp viper occurrence. Firstly, the urban areas are thermophilic habitats that could be actively selected by the asp viper, but this species does not occur in those zones, because of human persecution. Thus, urban areas could act as a sink due to snake killings by humans. Alternatively and more probably, urban areas do not represent an attractive habitat for vipers and the positive effect is probably due to similar "ecological preferences" by both vipers and humans. In fact, low altitude, gentle and sunny slopes are the preferred habitats for *V. aspis* in the Alps, but they are also the best sites to build small towns, to cultivate grapes or to perform tourism in mountain areas. This habitat convergence could reduce the availability of suitable sites for the asp viper leading to a conservation problem, since vipers are considered dangerous by people that are usual to kill snakes when they found it near urban areas.

Our results confirm data recorded by Saint Girons (1975) who stated that even in the narrow stripe in northern France where *V. aspis* and *V. berus* coexist they do not actually live in sympatry. Indeed, there are small populations juxtaposed without contact zones in a patchwork of microhabitats that respectively favour only one species at a time. Despite several ecological pressures could promote niche separation between the two species (e.g., feeding habits,



thermal ecology, daily activity, predatory pressure, and reproductive behaviour), Saint Girons (1975) recognized the differential predation risk to be the more relevant in his study area. Some of these factors could be important also in Italian Alps, but thermal and altitudinal gradients and habitat features might play a major role in niche separation in mountainous areas.

#### *Phylogenetic affinity and interspecific competition*

Niche separation between *V. aspis* and *V. berus* in the study area resembles that observed by Luiselli et al. (2007) for *V. aspis* and *V. ursinii*. In both cases the asp viper occurs in thermophilic low altitude areas whereas the adder and the Orsini's viper segregate in higher altitudes. Even if the asp viper can reach high altitudes in Italy (up to 2800 m in the Alps and up to 2200 m in the Apennines; Sindaco et al., 2006), it does not seem to compete with the other two vipers, as they use different microhabitats and, probably, microclimatic conditions (Luiselli et al., 2007; present study).

A similar pattern was highlighted in Spain by a recent study comparing three species of vipers (*V. aspis*, *V. latastei* and *V. seoanei*), where Seoane's viper is the vicariant of the adder (Martínez-Freiría et al., 2008). In this case, no sympatry was found between the phylogenetically distantly related viper, *V. seoanei*, and *V. aspis* or *V. latastei* (Martínez-Freiría et al., 2006), and areas of potential sympatry identified in this study between *V. seoanei* and the other two vipers were small.

These data and our results support the hypothesis that the asp viper does not compete with the *Pelias* group vipers (sensu Garrigues et al., 2005), whereas actively overlap with *V. latastei*, which belongs to the same phylogenetic group. Overall, these results indicate that interspecific competition among vipers in contact areas is negatively correlated with phylogenetic distance (Martínez-Freiría et al., 2008). This pattern fits with what foreseeable based on biogeographical hypothesis of European vipers

divergence from the Miocene (Lenk et al., 2001; Garrigues et al., 2005; Ursenbacher et al., 2006; Martínez-Freiría et al., 2008; Barbanera et al., 2009). Indeed, the contact zones between *V. aspis* and *V. latastei* resulted from a secondary meeting which followed the segregation on different refugia of common ancestors due to the ice expansion. Main refugia were located in the Mediterranean area: Southern Italy, Southern Spain, and Northern Africa. By contrast, the *V. aspis* and the *Pelias* groups suffered a separation in the early Miocene, that led to ecological adaptations respectively to warm and cold climates. The glacial events of the Quaternary period favoured the expansion of *Pelias* group southwards and the contemporary contraction of the *V. aspis* group within refugia. The opposite occurred during interglacial periods (Ursenbacher et al., 2006). The succession of latitudinal migrations led to the formation of relict populations. In this context, the *Pelias* populations of Italy and Spain are relicts confined in mountainous habitats within the asp viper distribution area, and as a consequence, competition between the two species should not be expected.

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