Spatial pattern, ecological niche, and interspecific competition of Viperidae in Korea.

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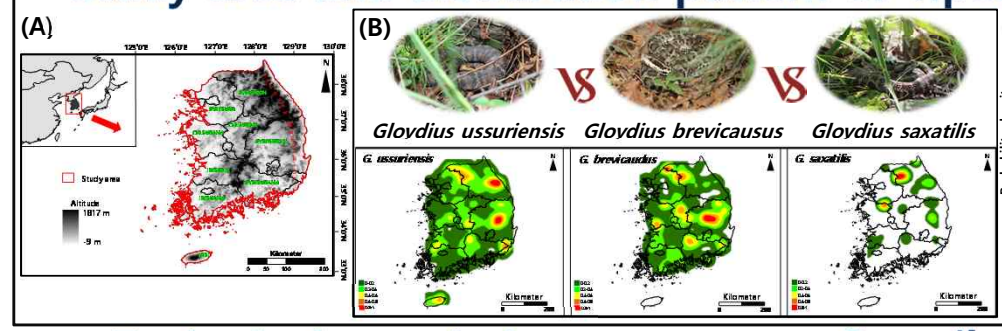
The aims of this study are to identity the spatial and ecological niches of sympatric three viper snakes in Korea and, based on this, to infer whether they actually compete with each other over spatial use.

Study area and distribution pattern of vipers

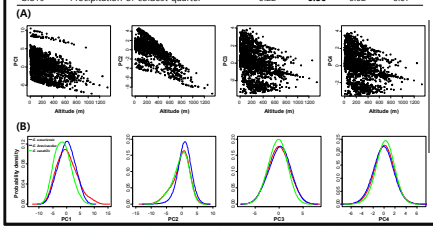


(A) The topographic map of South Korea and its largest island, Jeju-do. (B) Distribution map of the three species of viper and the density of observed individuals analyzed with a 0.019 degrees (about 2Km) cell size and search radius of 0.3 degrees using Kernal Density tool in the Arc Gis ver. 9.3. Note that the legends indicating the number of observed individuals are standardized for brevity and the maximum number of individuals represented by one vary among the species: 1197 individuals for *G. ussuriensis*, 633 for *G. brevicausus*, 100 for *G. saxatilis*. (C) Kernel density plots of the occurrence of the three species according to the altitude of South Korea.

Ecological correlation

Variable		PC1	PC2	PC3	PC4
% Variance explained		50.4%	26.5%	14.2%	5.4%
Eigenvalue		3.1	2.2	1.6	1.0
bio1	Annual temperature	**0.26**	0.22	0.19	-0.04
bio2	Mean diurnal range	-0.25	0.18	-0.14	**-0.37**
bio3	Isothermality	-0.10	0.15	-0.25	**-0.76**
bio4	Temperature seasonality	-0.30	0.11	0.04	**0.21**
bio5	Max temperature of warmest period	0.11	**0.38**	0.22	-0.02
bio6	Min temperature of coldest period	**0.31**	0.05	0.11	-0.06
bio7	Temperature annual range	**-0.30**	0.15	-0.01	0.06
bio8	Mean temperature of wettest quarter	0.16	**0.34**	0.22	0.03
bio9	Mean temperature of driest quarter	**0.29**	0.07	0.16	-0.20
bio10	Mean temperature of warmest quarter	0.15	**0.33**	0.27	0.07
bio11	Mean temperature of coldest quarter	**0.31**	0.10	0.12	-0.11
bio12	Annual precipitation	0.01	-0.32	**0.38**	-0.27
bio13	precipitation of wettest period	-0.24	-0.10	**0.36**	0.04
bio14	Precipitation of driest period	0.19	**-0.30**	-0.06	0.12
bio15	Precipitation seasonality	**-0.29**	0.11	0.22	0.10
bio16	Precipitation of wettest quarter	-0.17	-0.21	**0.41**	-0.17
bio17	Precipitation of driest quarter	0.22	**-0.30**	-0.03	-0.06
bio18	Precipitation of warmest quarter	-0.20	-0.17	**0.40**	-0.20
bio19	Precipitation of coldest quarter	0.22	**-0.30**	-0.02	-0.07

The results of the principal component analysis of the 19 bioclimatic variables extracted from the areas of South Korea. The first four PCs with eigenvalue larger than one were represented here. The percentages in parentheses indicate the amount of variation explained by each PC, and the components that were loaded most highly for each species occupies.



The patterns of association between the first four principal components and (A) altitude (B) The smoothed frequency distributions (kernel density plot) of the first four principal components that each species occupies.

Ecological niche overlap

	Mean of PI				Variance of PI		
Variables	Observed	Simulated[1]	ES[2]	P	Observed	Simulated	P
Altitude	**0.93**	0.56	4.87	< 0.0001	0.002	0.02	n.s
Land	**0.96**	0.38	3.60	< 0.0001	0.001	0.08	< 0.05
PC1	**0.94**	0.57	3.66	< 0.0001	0.002	0.03	< 0.05
PC2	**0.97**	0.45	4.06	< 0.0001	0.001	0.05	< 0.05
PC3	**0.97**	0.69	3.61	< 0.0001	0.001	0.02	< 0.001
PC4	**0.95**	0.46	3.53	< 0.05	0.001	0.06	< 0.05

The values of Pianka index (PI) showing the degree of overall niche overlap among the three species of viper in South Korea using the ECOSIM 7.0. Values of this index close to 1.0 indicate a complete overlap of niches between species, while values close to 0 represent clear niche separation between species.

Models summary

Species	Training AUC	Test AUC	Logistic threshold	Training omission	Test omission
G.ussuriensis	0.715	0.668	0.344	0.100	0.156
G.brevicausus	0.746	0.681	0.366	0.099	0.151
G.saxatilis	0.872	0.762	0.279	0.097	0.333

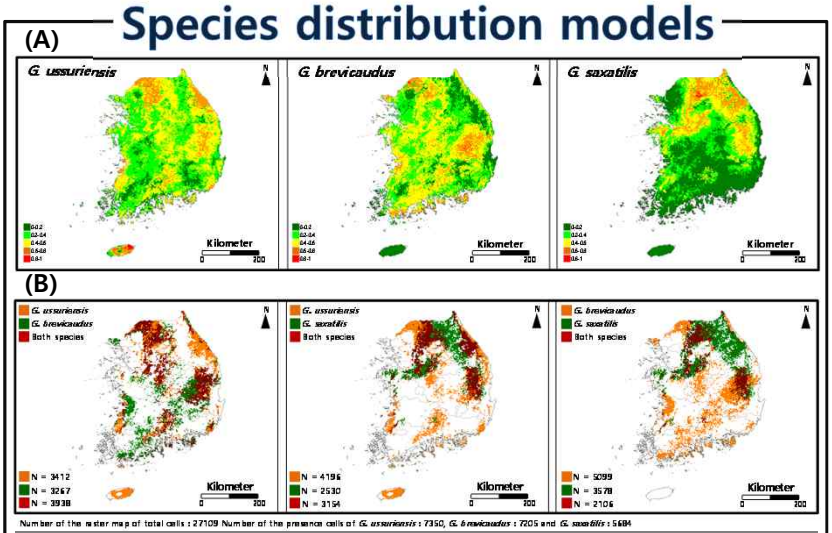
Summary of the Maxent models for the three species of viper in South Korea. The procedures were replicated 15 times using the Maxant vers. 3.3.3k.

Contribution of variable

Variable		*G. ussuriensis*	*G. brevicausus*	*G. saxatilis*
Alt	**Altitude**	**12.11 (8.0-17.0)**	**12.27 (8.4-16.9)**	13.08 (6.3-28.3)
Land	Land cover	6.30 (1.1-10.0)	3.21 (1.5-6.3)	4.73 (0.1-14.6)
bio1	**Annual temperature**	0.89 (0.2-3.1)	1.31 (0.1-5.6)	**14.57 (2.5-33.1)**
bio2	Mean diurnal range	7.45 (5.3-10.1)	4.67 (2.4-9.6)	0.11 (0.0-0.6)
bio3	Isothermality	2.04 (1.1-2.9)	4.23 (1.8-8.4)	13.40 (6.6-18.2)
bio4	**Temperature seasonality**	5.66 (3.2-8.9)	3.42 (1.5-5.6)	**17.29 (8.1-25.8)**
bio5	**Max temperature of warmest period**	**22.60 (19.6-27.2)**	**12.60 (4.8-23.0)**	0.16 (0.0-0.6)
bio6	Min temperature of coldest period	1.51 (0.2-2.8)	0.83 (0.3-2.2)	1.16 (0.0-3.5)
bio7	Temperature annual range	1.56 (0.6-2.6)	6.58 (4.1-9.8)	4.08 (2.2-6.7)
bio8	**Mean temperature of wettest quarter**	1.66 (0.3-5.4)	5.67 (0.2-16.1)	**14.63 (0.4-27.3)**
bio9	Mean temperature of driest quarter	0.49 (0.0-1.6)	2.17 (0.7-3.7)	0.03 (0.0-0.2)
bio10	Mean temperature of warmest quarter	1.01 (0.3-1.7)	3.56 (0.1-9.4)	0.27 (0.0-1.4)
bio11	Mean temperature of coldest quarter	0.08 (0.0-0.3)	1.87 (0.1-7.3)	0.60 (0.0-3.3)
bio12	Annual precipitation	2.69 (1.1-5.2)	4.17 (1.5-7.9)	0.19 (0.0-0.9)
bio13	**precipitation of wettest period**	**7.80 (4.6-11.2)**	**8.30 (5.0-11.4)**	6.89 (3.9-12.5)
bio14	Precipitation of driest period	5.77 (2.4-10.0)	4.41 (1.9-8.3)	1.63 (0.1-3.9)
bio15	Precipitation seasonality	4.66 (1.5-8.1)	2.36 (0.9-5.5)	3.68 (1.0-9.3)
bio16	Precipitation of wettest quarter	6.07 (2.9-8.8)	4.09 (1.6-6.6)	1.24 (0.1-6.1)
bio17	Precipitation of driest quarter	2.38 (0.4-8.2)	4.37 (1.5-8.8)	0.42 (0.0-1.1)
bio18	Precipitation of warmest quarter	3.72 (1.6-5.5)	4.36 (2.5-7.6)	1.68 (0.0-5.0)
bio19	Precipitation of coldest quarter	3.53 (0.5-8.9)	5.57 (1.6-10.4)	0.18 (0.0-0.7)

Average (minimum-maximum) percentage contribution of each variable for the 15 Maximum Entropy model for *G. ussuriensis*, *G. brevicausus* and *G. saxatilis* in the Korea.

Species distribution models



Number of the sister map of total cells : 27109 Number of the presence cells of *G. ussuriensis* : 7350, *G. brevicaudus* : 7205 and *G. saxatilis* : 5694

(A) Spatial prediction of the three species of viper in South Korea. Different colors represent the different degrees of occurrence probability (or habitat suitability). (B) The upper panel illustrates the overlap between predicted distributions of the three most partially distributed species in study area(The left panel, *G. ussuriensis* versus *G. brevicausus* : 14.5%, *G. ussuriensis* versus *G. saxatilis* : 11.6%, and *G. brevicausus* versus *G. saxatilis* : 7.8% of shared suitable cells, respectively). The logistic threshold of ten percentile training presence was applied to generate the presence/ absence map. The orange and green colors indicate the areas where only one species was predicted to be presence while the areas with brown color represent that both species are likely to occur together.

Discussion

Vipers partially overlapped in the study area, nevertheless they maintained distinct ecological niches, as assessed by the Pianka index. However we did not find direct factors about the effect of spatial distributions of vipers. Furthermore, further study should be conducted to include various topographic variables(e.g. slope, aspect, microhabitat, soil, solar radiation) or other variables (e.g. home range, food, reproductive strategies) for the study of vipers. We then may better understand the cause of spatial separation see in these Korean vipers.

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