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The relationships between land cover, climate and cave copepod spatial distribution and suitability along the Carpathians

THEMATIC SECTION
Spatial Simulation Models in Planning for Resilience

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SUMMARY

The distribution of subterranean copepods may reflect the persistence of cave assemblages in relation to the environmental health of the overlying landscape. Areas supporting groundwater fauna were established by modelling the persistence of seven copepod species using a geographical information system (GIS). Environmental drivers were found to influence subterranean copepod distribution in the caves of the Romanian Carpathians. Habitat-based modelling, using ordinary least squares regression and geographically-weighted regression to identify the significant predictors explaining copepod habitat suitability, predicted suitable areas for the selected taxa. The most constant predictor was land cover, a measure of human impact and climate change, followed by precipitation and altitude. The model performed well for the majority of analysed taxa, and the areas predicted as suitable for narrowly distributed taxa overlapped with observed distributions. GIS facilitated the prediction of suitable habitat, and also enabled spatial autocorrelation to be tested. The results of this study demonstrate the importance of sustainable management of the terrestrial surface in limestone areas in conserving copepod biodiversity.

Keywords: conservation, copepods, environmental drivers, geographically-weighted regression, habitat suitability models, subterranean habitats

INTRODUCTION

Ninety-seven per cent of all the fresh water available on Earth (excluding glaciers and ice caps) is stored in groundwater, the most extensive freshwater habitat in the world (Castany 1982). According to European Union (EU) Groundwater Directive (80/68/EEC, European Council 1980), groundwater is a valuable natural resource with a crucial role in providing water for human consumption and industrial or agricultural use. Because of groundwater's importance, much research on groundwater ecosystems has been carried out over the last two decades (Danielopol *et al*. 2000, 2009; Deharveng *et al.* 2009; Gibert & Deharveng 2002; Gibert *et al.* 2009; Stein *et al.* 2010; Moldovan *et al*. 2011; Schmidt & Hahn 2012). These ecosystems have value as an ecological indicator due to the specialized fauna adapted to subterranean life and their high rate of endemism (Castellarini *et al*. 2007; Danielopol *et al.* 2009; Deharveng *et al*. 2009; Galassi *et al*. 2009; Gibert *et al.* 2009). The socioeconomic value of groundwater ecosystems is due to the role played by invertebrates as ecosystem services providers with critical tasks in water quality improvement (such as natural water purification, bioremediation and water infiltration) (Boulton *et al.* 2008).

The Carpathian ecoregion stores around 80% of the Romanian freshwater reserves (excluding the Danube) (Bennett 2002), and approximately 30% of the Romanian groundwater resources are found within limestone aquifers (United Nations Environment Programme 2007). The Romanian Carpathians is a region rich in subterranean assemblages due to climatic diversity, abundance of caves at low altitudes and the patchy distribution of limestone (Moldovan *et al.* 2005). Copepods are dominant in groundwater habitats, including those of Romanian caves (Damian-Georgescu 1963, 1970; Moldovan *et al.* 2007, 2012; Meleg *et al.* 2011) and their assemblages are sensitive to human-induced perturbations of water quality and the groundwater hydrological regime (Dole-Olivier *et al.* 1994; Malard *et al.* 1998; Paran *et al.* 2005; Galassi *et al*. 2009; Moldovan *et al.* 2011). At the same time, the high abundance of copepods, their heterogeneous distribution in groundwater, and their sensitivity to pollutants suggest that they

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Table 1 Environmental variables used in modelling.

Variable	*Code*	*Unit and classes*	*Type*	*Source*
Altitude	ALT	From 65 to 1556 m asl	Quantitative	Geo-spatial.org (http://earth.unibuc.ro)
Mean annual temperature	TMA	From 2.60 to 11.30 °C	Quantitative	WORLDCLIM database (Hijmans *et al.* 2005)
Mean annual precipitation	PMA	From 620 to 939 mm yr^{-1}	Quantitative	WORLDCLIM database (Hijmans *et al.* 2005)
Geology	GEO	3 classes: 1 = karstic rocks (limestones and dolomites); 2 = karstic rocks mixed with non-karstic rocks and 3 = non-karstic rocks	Qualitative	Geological Institute of Romania (http://www.igr.ro)
Land cover	CLC	9 classes: 3 = broad-leaved forest; 5 = complex cultivation patterns; 7 = coniferous forest; 9 = discontinuous urban fabric; 13 = fruit trees and berry plantations; 15 = land principally occupied by agriculture, with significant areas of natural vegetation; 17 = mixed forest; 19 = pastures; 21 = transitional woodland-shrub.	Qualitative	Geo-spatial.org (http://earth.unibuc.ro)
Hydrographic basin	HDB	14 basins: 51 = Arieş, 52 = Caraş, 53 = Cerna, 54 = Crişul Alb, 55 = Crişul Negru, 56 = Crişul Repede, 57 = Dunăre, 58 = Ialomiţa, 59 = Jiu, 60 = Mureş, 61 = Nera, 62 = Olt, 63 = Someş, 64 = Timiş	Qualitative	National Institute of Hydrology and Water Management (http://www.inhga.ro)

would be useful bioindicators of underground-surface water connectivity and groundwater quality (Malard *et al.* 1994; Di Lorenzo *et al.* 2005; Pipan *et al.* 2006; Moldovan *et al.* 2013).

Small-scale studies in the Romanian Carpathians indicate that copepod distribution in groundwater is related to electric conductivity of the water and the transition time of the water within the void network (Moldovan *et al.* 2007, 2012; Meleg *et al.* 2011). Forest cover seems to be the main environmental determinant of the diversity and abundance of cave aquatic populations (Meleg *et al.* 2012). Here we test the latter observation at a larger scale, based on distribution modelling of cave copepods. Our aim was to assess the applicability and efficiency of GIS in modelling cave-population persistence by mapping assemblage distributions in caves and applying customized habitat suitability models.

Predictive modelling of species' distributions is a topic of great interest in ecology, biogeography and conservation biology (Whittaker *et al.* 2005; Rodríguez *et al.* 2007; Elith *et al.* 2011) when used to model the probabilities of occurrence of species (Segurado & Araújo 2004; Elith *et al.* 2006). A common approach to predictive modelling relates known occurrences of species to climate and other environmental variables, and the modelled distribution of species can be projected onto an interpolated climate surface under current and predicted climate scenarios (see for example Yates *et al.* 2010).

Geographical information systems (GISs) are a useful tool for better understanding and visualizing such distribution data (see Schmitt & Rákosy 2007; Costa *et al.* 2008; Martínez-Freiría *et al.* 2008). GIS habitat suitability modelling is also useful for determining a site's suitability for harbouring different species based on its environmental features (Rodríguez *et al.* 2007). Predictive modelling has been successfully implemented for plants, invertebrates, reptiles, amphibians, birds and mammals (Bio *et al.* 2002; Brotons *et al.* 2004; Finch *et al.* 2006; Linkie *et al.* 2006; Kopp *et al.* 2010; Elith *et al.* 2011; Simpson & Prots 2013), but, to our knowledge, species distribution modelling in groundwater has been attempted only for hypogean populations from the Jura Mountains (France) (Castellarini *et al.* 2007), where it explained an average of 36% of the variability in each species' distribution. There hydraulic conductivity, geology, altitude and time since the last glacial episode were important in explaining hypogean distributions (Castellarini *et al.* 2007). The paucity of attempts to model species distribution in subterranean habitats is attributable to the sampling methodology (fauna inhabiting inaccessible fissures, collected indirectly by pumping the interstitial water or by sampling the water percolating through the void network in caves; Gibert 2005), distribution ranges (real distribution ranges of some species poorly known due to cryptic speciation in subterranean environments; Lefébure *et al.* 2006) and the difficulty of monitoring cave environments at large scales.

Our results are discussed within the context of how climate variables related with other environmental drivers may affect the future distribution of groundwater biodiversity across Carpathians and these measures can be used as an indicator of environment health.

METHODS

Building the database

This study is focused on groundwater habitats, void networks and pools, in caves of the Romanian Carpathians. Point-sampled data for biological (Appendix 1, Table S1, see

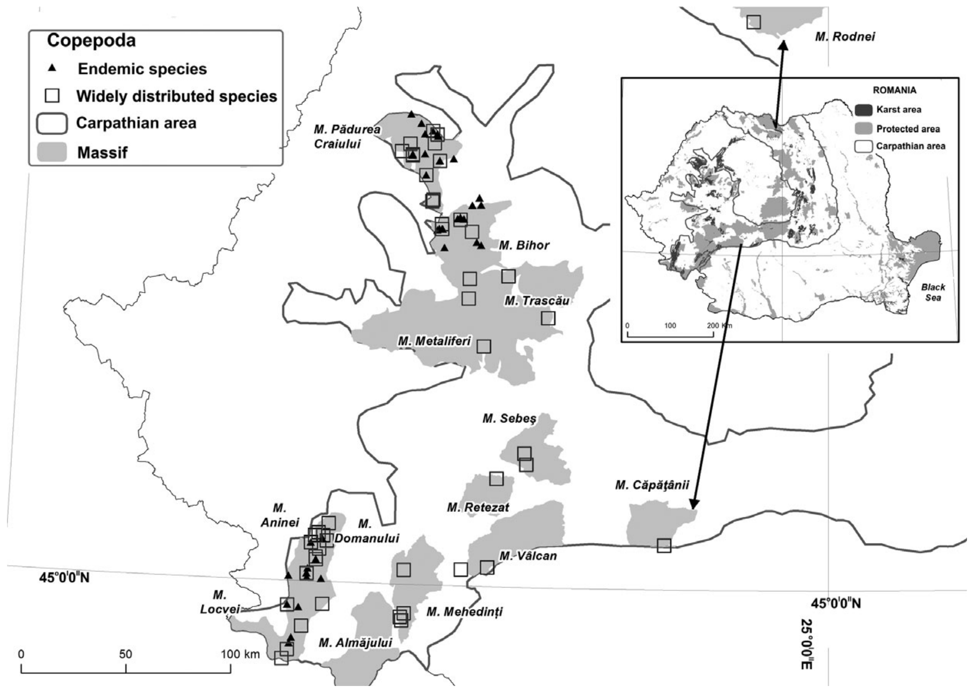

Figure 1 Distribution of modelled copepods across the Romanian Carpathians. Protected areas layer available from URL http://www.mmediu.ro/protectia_naturii/protectia_naturii.htm. (last access date on December 1, 2011)

supplementary material at Journals.cambridge.org/ENC) and habitat variables (Table 1) were gathered from several sources. Three quantitative and three qualitative environmental variables that describe the surface-cave ecosystem were included in the model.

Copepod distribution data were compiled from different sources, including: (1) 38 published sources; (2) existing databases of the 'Emil Racoviță' Institute of Speleology, and (3) personal surveys (the list of all references is available on request). Two ecological categories of copepods were considered, hypogean and epigean, based on the copepods restricted to groundwater and surface habitats, respectively. Species presence data were georeferenced as point-sampled data using Google Earth Pro and ArcGIS Desktop (ESRI [Environmental Systems Research Institute] 2010). The final list includes 238 records (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC). The minimum number of records for a species was one and the maximum was 18. The habitat suitability model was applied at the species and genus levels for the seven taxa having more than 10 entries in the database (Fig. 1, Table 2).

For accuracy, all data were projected in the Stereo70 coordinate system using the Dealul_Piscului_1970 datum between the spatial scales of 1:100 000 and 1:200 000.

Linear regression analysis

To obtain the pattern of ecological conditions for each species location, linear regression analysis (ordinary least squares [OLS] and geographically-weighted regression [GWR]) was performed using spatial statistics in ArcGIS 9.3.1 (ESRI 2010). In the first step, OLS was used to model and examine the statistically significant factors behind observed spatial distribution patterns. Once the significant factors were selected, the GWR was computed over a spatial scale based on neighbours' measures in order to remove the assumption of spatial stationarity in the distribution modelling. The statistically significant variables identified by the linear regression analysis were kept for the habitat suitability modelling (Fig. 2).

The significant factors were selected by computing OLS. Akaike's information criterion (AIC) (Akaike 1974) was used to select the most parsimonious model. The Jarque-Bera test was used to evaluate the goodness of fit of the models, indicating if the residual values (the over- and under-predictions) had a normal distribution. If they did not, the model was biased. Multicollinearity was detected by calculating the variance inflation factor (VIF), an index measuring how much the variance of the estimated regression coefficient increased because of collinearity. The VIF ranges from 1.0 to infinity, and we considered its threshold value should be less than 7.5 to avoid multicollinearity (Kenneth *et al.* 2013). Environmental variables with a VIF greater than 7.5 were removed one by one until the VIF indicated the model was not biased. An adjusted R^2 value was used to measure the proportion of the variation in the dependent variable (species) accounted for by the environmental variables.

OLS allowed simultaneous processing of quantitative and qualitative variables. For all qualitative variables integer codes were associated with their values, having a minimum of three integer codes per variable (Table 1). The analysis took into account the unique identification of each database record, which further was associated with all the predictors' values. In this regard, VIF was very useful in discarding variables that contained redundant information.

The GWR created a coefficient surface for each environmental variable showing where the relationships were

Table 2 Number of sampling sites, number of copepod species, and number of hypogean and endemic copepod species for each sampled Carpathian unit included in habitat suitability modelling.

Major Carpathian units	*Regional units*	*Karst massifs*	*Number of sampling sites*	*Total number of copepod species*	*Total number of hypogean copepod species*	*Total number of endemic copepod species*
Western unit	Apuseni	Bihor	17	12	9	7
		Pădurea Craiului	18	14	7	3
		Trascău	1	2	1	0
		Metaliferi	4	3	2	0
Southern unit	Banat	Almajului	1	1	0	0
		Aninei	15	12	8	3
		Domanului	2	3	2	0
		Locvei	5	8	5	4
	Eastern unit	Căpăţânii	1	2	1	0
		Sebeş	2	3	1	0
	Central unit	Mehedinţi	4	8	1	0
		Retezat	1	6	0	0
		Vâlcan	1	3	1	0
Eastern unit		Rodnei	1	1	0	0

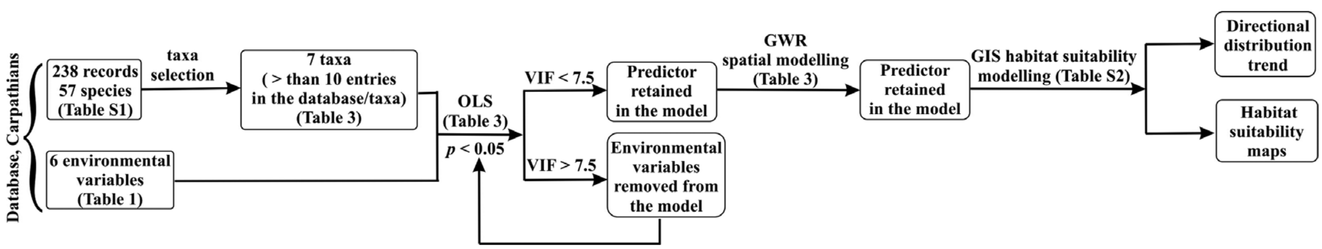

Figure 2 Simplified diagram showing the statistical analyses performed to model taxa habitat suitability. OLS = ordinary least squares; VIF = variance inflation factor; GWR = geographically-weighted regression.

strongest. As for OLS, an AIC value and adjusted R^2 were computed to test for good model performance. The goodness of fit was tested using the spatial autocorrelation (Morans *I*) tool, in order to check for the spatial autocorrelation of model residuals. When a good model was found, the residuals reflected random noise (Goodchild 1986). The correlation coefficients were estimated using nearby feature values. Adaptive kernel estimation was used in the present models, with the number of neighbours ranging from 5 to 15, in order to determine the best model (Fotheringham *et al.* 2002).

Habitat suitability model

The statistically significant variables were used to develop habitat suitability models and predict species-environment relationships and spatial patterns across spatial scales. Năpăruş and Kuntner (2012) developed a habitat suitability model using the ModelBuilder environment from ArcGIS Desktop 9.3.1 (ESRI 2010). We applied the same model for seven different copepod taxa to visualize their directional distribution trend and the areas with high, moderate and low habitat suitability.

The directional distribution trend was computed for each taxon as an elliptical area centred on the mean of all localities inhabited by that taxon. We used the option with three standard deviations to maximize the potential species distribution to cover *c.* 99% of all feature centroids (Mitchell 2005). The model shows the central tendency and its spatial orientation for each species' distribution as an indication of potential trend dispersion. The directional distribution represents a species' potential target area for habitation (Năpăruş & Kuntner 2012). In the case of copepods, we assumed that each taxon's potential habitat exhibited preferences for a corridor with a total span of five degrees of longitude. In this potential distribution area, we extracted the values for the environmental predictors corresponding to each taxon's database records in order to obtain their frequency and then to classify them as high, moderate or low frequency. In the cases of two widely distributed taxa, when only two classes were depicted we preferred to classify the values as high and moderate. These frequency values were used to identify, within the species directional distribution, similar values, which were reclassified to represent habitat suitability (reclassified as high = 3, moderate = 2 and low = 1). In order to obtain a scale of suitability from 1 (low) to 3 (high), we used the weighted sum tool, by multiplying the designated field values for each environmental parameter with the specified weight. The weights for the habitat suitability were assigned by dividing 1.0 (100%) among the resulted correlated parameters. 'NoData' values were ignored. If the

Table 3 Summary of OLS and GWR statistical models for seven copepod taxa in groundwater habitats of the Carpathians (all data are statistically significant at $p < 0.05$). OLS = ordinary least squares; VIF = variance inflation factor; GWR = geographically-weighted regression; PMA = mean annual precipitation; TMA = mean annual temperature; ALT = altitude; CLC = land cover. [1]Hypogean taxa. For harpacticoids, we used Wells (2007) and, for cyclopoids, Dussart and Defaye (2006). Each selected group is considered as an ecological unit, which is not necessary a taxonomically defined taxon. **Acanthocyclops* sp. includes the following species currently unified in the *kieferi* group of this genus: *A. balcanicus bisaetosus*, *A. deminutus*, *A. kieferi*, *A. milotai*, *A. plesai*, *A. propinquus*, *A. reductus*, and *A. transylvanicus*. ***Bryocamptus (Limocamptus)* sp. includes the closely-related *B. (L.) echinatus*, [1]*B. (L.) dacicus* and *Pilocamptus georgevitchi*, which differ morphologically from the '*zschokkei*' group by their three-segmented leg 1 structure. ****Bryocamptus (Rheocamptus)* sp. includes species with reduced leg segmentation and armature: *B. (R.) typhlops* and *B. (R.) unisaetosus*. *****Bryocamptus zschokkei* group includes species characterized by untransformed segmentation and armature: *B. (B.) pygmaeus*, *B. (B.) spinulosus*, *B. (B.) zschokkiei caucasicus*, *B. (B.) zschokkei tatrensis*, and *B. (B.) zschokkei zschokkei*. ******Elaphoidella* sp. includes: *E. phreatica*, *E. phreatica pseudophreatica*, *E. putealis*, *E. romanica* and *E. winkleri*.

Taxa	*OLS*							*GWR*	
	Predictor retained in the model	*β-coefficient*	*VIF*	*AIC*	*Adjusted R^2*	*AICc*	*Adjusted R^2*	*Spatial auto-correlation*	*No. of neighbours*
[1]*Acanthocyclops* sp. *	CLC	3.26	1.02	458.42	0.21	341.32	0.98	Quasi random	15
	PMA	–0.47	1.02						
Bryocamptus (Limocamptus) sp. **	CLC	2.46	6.08	57.65	0.98	126.64	0.58	Quasi random	10
	ALT	–0.12	2.68						
Bryocamptus (Rheocamptus) sp. ***	ALT	0.14	3.78	245.51	0.55	169.46	0.83	Random	5
Bryocamptus zschokkei group ****	TMA	33.62	1.44	340.42	0.27	128.41	0.75	Random	10
[1]*Elaphoidella* sp. *****	CLC	5.39	1.47	138.37	0.31	170.83	0.67	Random	5
Megacyclops viridis	PMA	–0.50	1.10	200.96	0.35	128.72	0.87	Quasi random	10
[1]*Spelaeocamptus spelaeus*	CLC	2.86	1.03	129.47	0.27	145.11	0.26	Random	10

species was correlated with two environmental parameters, we combined them by assigning equal weights (0.5). In the case of a single environmental parameter, the given weight value was unity.

The model was finalized by fitting the habitat suitability dot representation to a local scale with a radius of nine cell units (720 m) by using focal statistics analysis (Guisan & Thuiller 2005). All cells whose centre fell inside this radius were included in processing the neighbourhood.

Among the seven habitat suitability maps, two are given here as examples (the hypogean species *Acanthocyclops* sp. and the epigean species *Bryocamptus zschokkei*) (other maps are provided in Appendix 1, Figs S1–S5, see supplementary material at Journals.cambridge.org/ENC).

RESULTS

Except for *Spelaeocamptus spelaeus* (adjusted $R^2 = 0.26$), the GWR results explained more than 50% of the taxon-environment relationship (Table 3). Of the six predictors included in the model, the main drivers were temperature and precipitation for epigean species, while land cover was significant mainly for hypogean taxa.

Scatter plot matrices to explore bivariate cause-effect relationships between environmental parameters through β-coefficients recovered only a positive correlation between altitude and mean annual precipitation (PMA), and negative correlations between altitude and mean annual temperature (TMA) and between TMA and PMA (Fig. 3).

The residuals reflected random noise for *Bryocamptus (Rheocamptus)* sp., *Bryocamptus zschokkei* group, *Elaphoidella* sp. and *Spelaeocamptus spelaeus*, and quasi-random noise for *Acanthocyclops* sp., *Bryocamptus (Limocamptus)* sp. and *Megacyclops viridis*, as indicated by the spatial autocorrelation analysis

Acanthocyclops sp., *Bryocamptus (Limocamptus)* sp., *Elaphoidella* sp. and *S. spelaeus* had positive correlations with land cover (CLC) (Table 3), showing a preference for areas covered by broad-leaved and mixed forests (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC). *S. spelaeus* was also correlated with areas covered by agricultural fields. Areas with discontinuous urban fabric, pastures, fruit tree plantations and transitional woodland-shrub were associated with low and moderate probabilities of harbouring copepod species. *Megacyclops viridis* and *Acanthocyclops* sp. had negative correlations with PMA (Table 3). *M. viridis* showed preferences for areas with precipitation of 630–865 mm yr^{-1}, with high probabilities of being encountered in areas with precipitation of 710 mm yr^{-1}. For *Acanthocyclops* sp. the most suitable areas were those with precipitation of 650–800 mm yr^{-1}. This species had a low probability of occurrence in areas with high precipitation rates (810–860 mm yr^{-1}). The epigean *Bryocamptus zschokkei* group was strongly correlated with temperature, with the probability

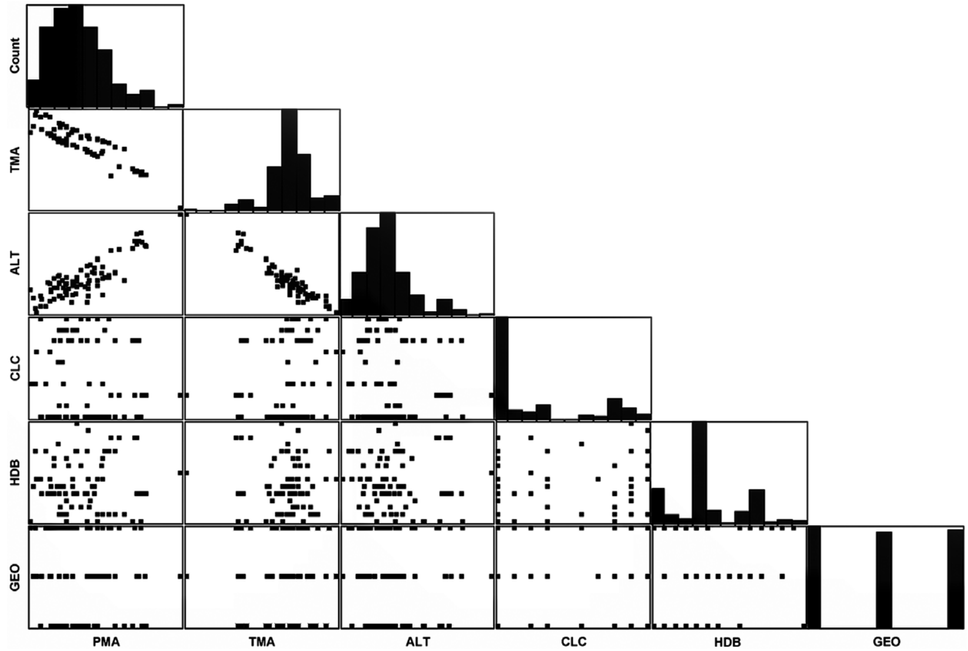

Figure 3 Scatter plot matrices displaying relationships among the environmental parameters for all 238 records in the database. PMA = mean annual precipitation; TMA = mean annual temperature; ALT = altitude; CLC = land cover; HDB = hydrographic basin; GEO = geology.

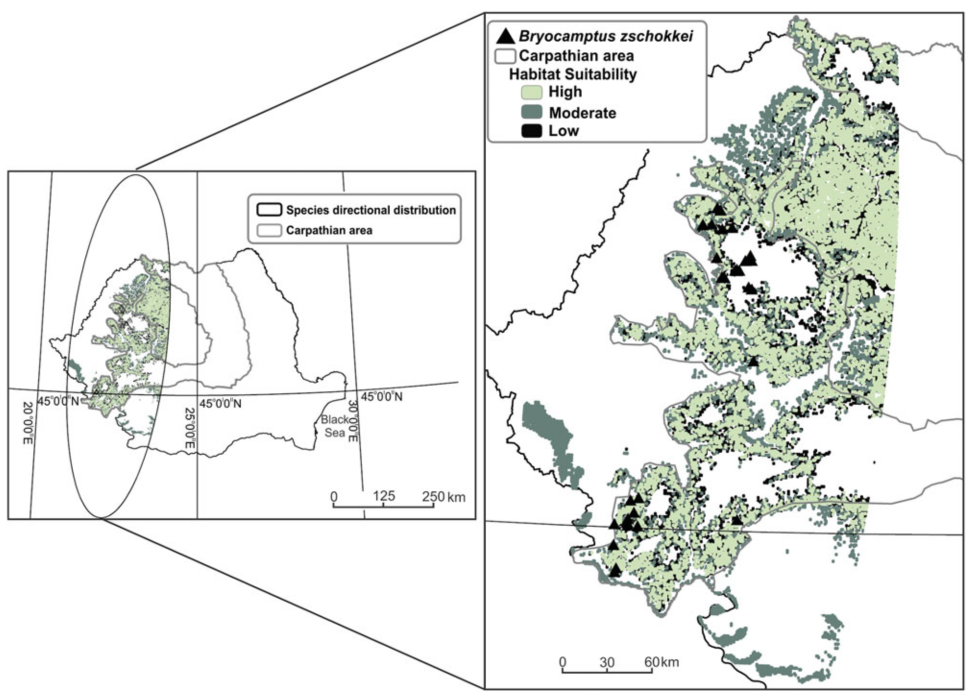

Figure 4 Habitat suitability map for the epigean *Bryocamptus zschokkei*. Triangles = current specimen records. Predicted suitable habitats are represented by light grey (high probability of taxa occurrence), dark grey (moderate probability of taxa occurrence) and black dots (low probability of taxa occurrence).

of occurrence increasing from 8.2 to 9.1 °C (Fig. 4). The altitude was important for the other two *Bryocamptus* groups (*Limocamptus* and *Rheocamptus*), the first having high chances of being encountered in areas with elevations of 274–540 m above sea level (asl), while the second had a wider elevation range of 344–1269 m asl.

All the considered taxa were sampled from the Romanian Carpathian caves, but the areas predicted to be suitable were not consistent with the observed distributions in the limestone areas; all taxa had high probabilities of occurrence outside these areas. For the *B. (Limocamptus)* species, a high probability of suitable habitats was detected along a north-south distribution outside the Romanian Carpathians, in areas with lower elevation (namely south of Banat and more scattered suitable habitat in the north-west of Romania) (Appendix 1, Fig. S1, see supplementary material at Journals.cambridge.org/ENC). The *B. (Rheocamptus)* species have the largest areas of suitable habitat distributed north-east to south-west (Appendix 1, Fig. S2, see supplementary material at Journals.cambridge.org/ENC). The model predicted large areas of suitable habitat with high probabilities of *B. zschokkei* group occurrence, with a north-south distribution (Fig. 4). *M. viridis*, currently widespread in Romania, showed mainly moderate probabilities of occurrence

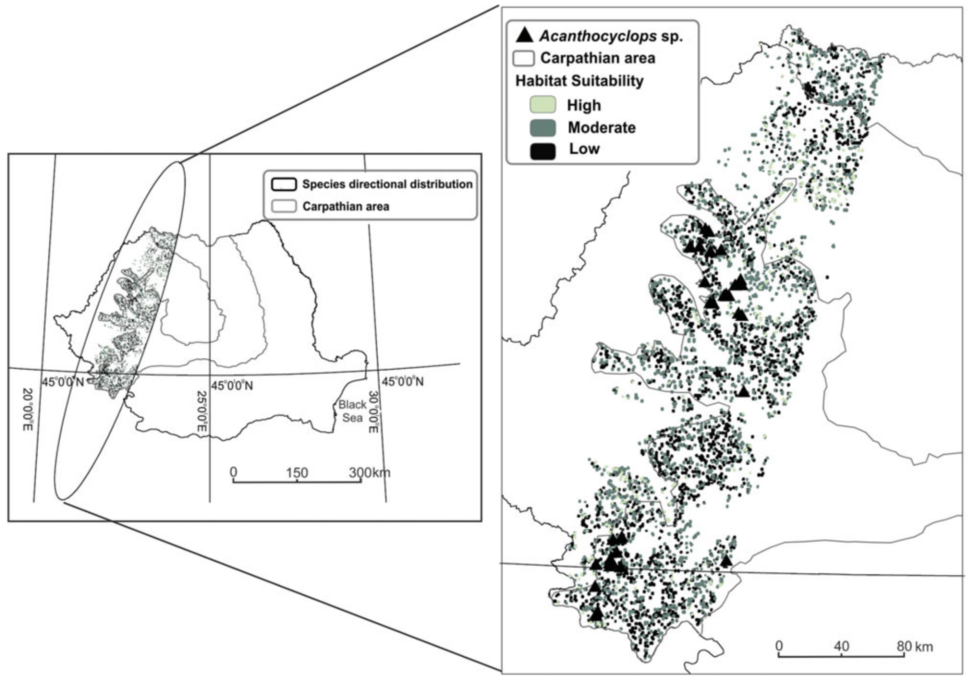

Figure 5 Habitat suitability map for the hypogean *Acanthocyclops* sp. Triangles = current specimen records. Predicted suitable habitats are represented by light grey (high probability of taxa occurrence), dark grey (moderate probability of taxa occurrence) and black dots (low probability of taxa occurrence).

in western Romania, distributed along a north-west to south-east axis (Appendix 1, Fig. S3, see supplementary material at Journals.cambridge.org/ENC). Compared to epigean species, the suitable areas predicted by the habitat suitability model overlapped more closely the observed distribution of hypogean taxa *Acanthocyclops* sp. (Fig. 5), *Elaphoidella* sp. (Appendix 1, Fig. S4, see supplementary material at Journals.cambridge.org/ENC) and *S. spelaeus* (Appendix 1, Fig. S5, see supplementary material at Journals.cambridge.org/ENC), whose more restricted predicted distribution was oriented towards limestone areas, the first two species being distributed along a north-west to south-east axis and the last along a north-east to south-west axis.

DISCUSSION

Cave assemblages enclosing epigean and hypogean species were useful in predicting the surface environment health related to land-use and climate variables. The habitat suitability model was easily applied because of its simple customizing process, high degree of visualization, and adaptivity for each taxon's requirements. Based on spatial autocorrelation analysis, the performance of the final models was adequate, reflecting the random and quasi-random noise characteristic of good models. According to Osborne *et al.* (2007) and Bacaro *et al.* (2011), spatial autocorrelation in species distribution modelling, as a common property of ecosystems, is an important feature usually missed or inadequately considered.

Overall our model achieved a good fit, with GWR adjusted R^2 values approaching 1. The low adjusted R^2 in *S. spelaeus* case is not unexpected, knowing that species distribution modelling attempted for hypogean populations from the Jura Mountains explained 36% of the average deviance of hypogean species distribution (Castellarini *et al.* 2007). Our results suggest a proper selection of predictor variables in most of the cases. In the present study, depending on taxon requirements, four out of six predictors were retained in the habitat suitability models: altitude, mean annual precipitation, mean annual temperature and land cover.

The north-west to south-east distribution, with low probability of occurrence outside the known distribution range of *Acanthocyclops* sp., is probably due to the narrow niche requirements of this highly diversified and endemic genus (Galassi *et al.* 2009). All the species belong to the *kieferi* species complex, a diversified group within the groundwater of Romania (Iepure & Defaye 2008). The distribution of *A. transylvanicus* was not found to be dependent on the local precipitation (Meleg *et al.* 2012), suggesting the importance of scale when assessing biodiversity, as emphasized by Stoch and Galassi (2010).

Our model showed a narrow range of suitable areas for *Elaphoidella* sp. and *S. spelaeus*, both with probabilities of occurrence along the western extremities of the Romanian Carpathians. The predicted probabilities of occurrence outside limestone areas for both species, not overlapping their current range in caves, show their possible distribution in other groundwater habitats, such as interstitial waters of surface rivers or springs (Damian-Georgescu 1970). For *S. spelaeus*, the areas predicted to be most suitable were consistent with the observed site-specific distribution in caves of the western Carpathians (Fiers & Moldovan 2008).

For the hypogeans *Acanthocyclops* sp., *Elaphoidella* sp. and *S. spelaeus*, the predicted suitable habitats were more or less restricted to the observed distribution patterns. Their distribution may reveal limited ability to disperse and exploit hydrological connectivity through migration, as in the Jura Mountains (Castellarini *et al.* 2007). There the occurrence

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of *E. phreatica* is related to high elevation, unlike in the present study where elevation was not a significant predictor for *Elaphoidella* species, including *E. phreatica*. Only the epigeans *Bryocamptus (Limocamptus)* sp. and *Bryocamptus (Rheocamptus)* sp. had distributions correlated with elevation. For the *B. (Limocamptus)* group, a high probability of suitable habitats occurred outside the limestone areas of the Romanian Carpathians at lower elevations, suggesting either this sub-genus' preference for non-limestone habitats (Damian-Georgescu 1970), or its occurrence is the result of being washed from the surface into the cave. The *B. (Rheocamptus)* group showed the largest spectrum of suitable habitats, both representatives occurring in a wide range of habitats (mosses, springs, wells, peat bogs and groundwater). Although *B. zschokkei* has occurred throughout the temperature range, it was the only group where occurrence was correlated with temperature. The habitat suitability model predicted only rather low probabilities of suitable habitats for *M. viridis*, model performance was probably influenced by the cosmopolitan distribution of this species encompassing a large number of ecological features across their distribution range (Osborne *et al*. 2007).

Climate variables were directly related with the epigean taxa, and were the most important drivers explaining their distribution in caves. The modelled suitable habitats underline their transitory status within the caves, as has been determined at smaller spatial scales (Meleg *et al*. 2012; Moldovan *et al*. 2012). Their observed sensitivity to changes in temperature or precipitation indicate epigean taxa might find protection from climatic disturbance inside caves. Their persistence within cave assemblages might impact the resident hypogean assemblages, with biotic interactions leading to ecological and populations' instability; narrowly-distributed hypogean taxa more susceptible to ecological disequilibrium and habitat loss (Cardoso *et al*. 2010) will either adapt or become endangered.

Our work emphasizes for the first time the importance of land use and anthropogenic impact (Vandewalle *et al.* 2010) on habitat suitability for groundwater copepods. For the hypogean *Acanthocyclops* sp., *Bryocamptus (Limocamptus)* sp., *Elaphoidella* sp. and *S. spelaeus*, we found low and moderate probabilities of occurrence in areas where the above-cave habitats were covered by sparsely vegetated areas, fruit tree plantations within a discontinuous urban matrix, or pastures. The forests and land used in traditional agriculture appear important for underground copepod population persistence.

Deforestation is directly linked to climate changes that lead to temperature increases, shifts in precipitation patterns and drying out of the vegetation (Davin & de Noblet-Ducoudré 2010). The environmental parameters mirrored the responses of groundwater communities to surface-groundwater dynamics when more than one parameter was in the final model. For example, *Acanthocyclops* sp. display preferences for forested areas and moderate amounts of precipitation.

Both the forest and soil play an important role in cave evolution and ecosystem dynamics, as sources of organic matter that concentrate within the void network and in pools populated by copepods (Williams 2004; Meleg *et al*. 2012). Water balance is also important in determining and sustaining the terrestrial vegetation, and thus the land cover (Neilson 1995). The water input has a major role in limestone dissolution, and in cave and fissure formation as suitable habitats for copepod populations. Water also governs the dispersal of organisms and plays an important role in the transportation of organic matter and epigean organisms below ground (Moldovan *et al*. 2012).

Intensive cultivation also raises concern for use of nitrogen-rich fertilizers and pesticides, such substances being harmful below ground when quickly washed into caves, as happens when the filtration process is ineffective due to soil erosion. Organic pollution leads to depletion of subterranean communities (Hancock *et al.* 2005) and groundwater copepod communities are no exception. GIS modelling revealed that hypogeans are more endangered cave assemblages than those of epigeans, because they have narrow distribution ranges and the local effect of surface pollution would be more intense. Pollution at the aquifer scale impacts the inhabited voids by generating heterogeneous patches with different degrees of alteration, ecological disequilibrium and subterranean fauna depletion or extinction (Mösslacher & Notenboom 1999).

The low predicted occurrence of studied taxa in areas facing anthropogenic pressure through land-use changes associated with climate variations emphasizes the potential use of copepods as bioindicators for the dynamic surface-groundwater system. Groundwater invertebrates also maintain a high water quality through water purification, bioremediation, and water infiltration and transport (Boulton *et al*. 2008; Griebler *et al*. 2010). Their persistence below ground is an indirect measure of surface-groundwater system health.

Given its computational efficiency and reliability, GIS is a useful tool for identifying endemism and biodiversity hotspots at local and regional scales. GWR and the designed habitat suitability model provided a framework for coupling distribution patterns to ecosystem dynamics for both epigean and hypogean species. Both human induced stressors across space and climate change across time may act as ecological barriers for cave assemblages that may lead to disturbed subterranean habitats.

CONCLUSION

This study provides evidence for the importance of managing the landscape in limestone areas to conserve the groundwater resources and copepod biodiversity. We propose a model for groundwater protection based on the sustainable use of the surface land. Surface land management should be oriented towards promoting traditional agricultural practices and soft deforestation, and reforestation when needed. Most of the known distribution of the analysed communities are within protected areas (national and natural parks and Natura 2000 sites) where sustainable practices are promoted according to EU Habitats Directive (92/43/EEC; European Commission

2013) and Groundwater Directive (2006/118/EC; European Council 2006), as well as Romanian Law no. 49/2011 regulating natural protected areas, conservation of natural habitats, wild flora and fauna in Romania and the Romanian Forest Code. We have identified areas not included in the current protected areas that should also be managed in order to preserve the groundwater and its fauna. Our assessment is relevant in understanding the potential impact of the key driving forces of cave assemblages' distribution as a proxy to the interconnected environmental surface-subterranean systems in limestone areas.

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