

## SYMPATRY WITHOUT CO-OCCURRENCE: EXPLORING THE PATTERN OF DISTRIBUTION OF TWO *HELIX* SPECIES IN GEORGIA USING AN ECOLOGICAL NICHE MODELLING APPROACH

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### ABSTRACT

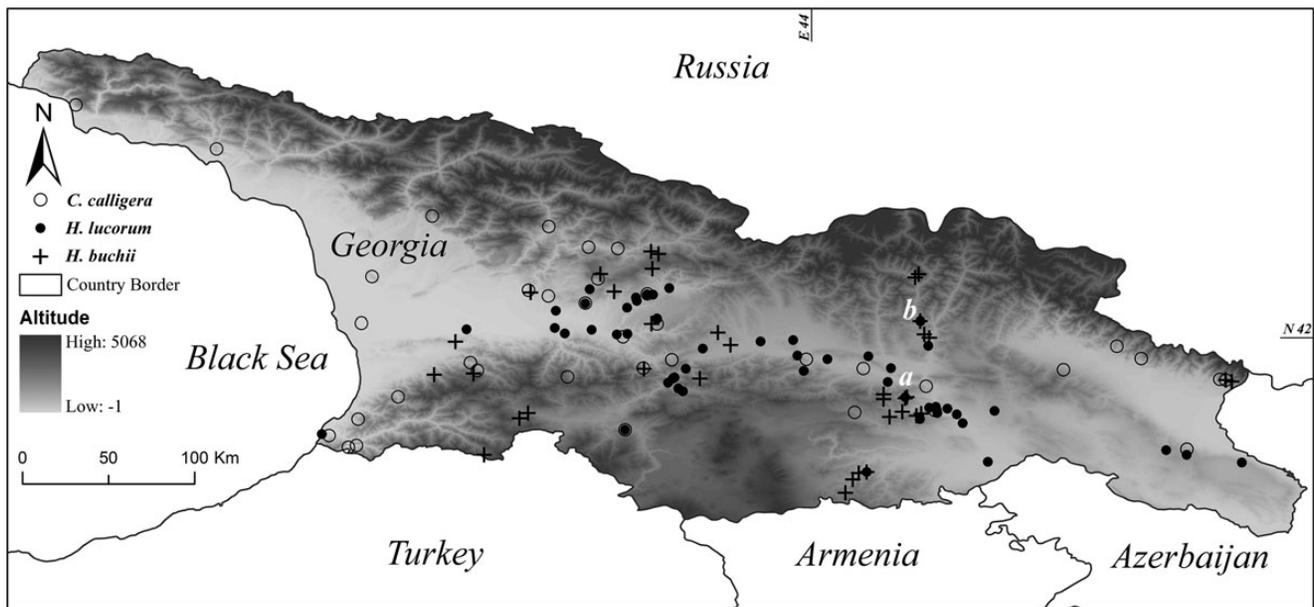
Two species of the genus *Helix* are widespread in Georgia: *H. lucorum* has a Mediterranean distribution whereas *H. buchii* is a Caucasian endemic typically associated with broadleaved forests. In spite of their sympatry within Georgia, they are never syntopic. Furthermore, in contrast with *H. buchii*, *H. lucorum* is mainly found in areas subject to human disturbance. Another large helicoid species, *Caucasotachea calligera*, is widespread in Georgia and usually co-occurs with either *Helix*. The distribution patterns of these species suggest that interspecific competition might play an important role in shaping the distribution of the two *Helix* species. In order to see whether their ecological niches were different enough to provide such a distribution pattern, I used predictive ecological niche models (ENM) based on the Maximum Entropy algorithm. ENMs showed that the niches of these species in Georgia were significantly different but not fully separated (~15–36% overlap). The distributional pattern of *H. lucorum* should not be considered truly natural in Georgia and may be anthropogenic. The fact that the two *Helix* species never co-occur may result from factors other than ecological niche differentiation at any macro scale. Since competition remains the most useful and informative assumption to explain the distributional pattern of these congeneric species, microhabitat requirements also need to be tested as a potential driver.

### INTRODUCTION

Two large helicoid species *Helix lucorum* Linnaeus 1758 and *H. buchii* Dubois de Montpéroux, 1839 are common in Georgia. *Helix lucorum* is a typical circum-Mediterranean snail (probably coming from the areas around the Adriatic Sea) and approaches the Caspian Sea in its eastern range. It is usually one of the most common and abundant snails within its native distributional area (Yildirim, Kebapci & Gumus, 2004) and is widespread in Georgia. The species is found in almost all kinds of habitats near or within human-modified landscapes and can be regarded as synanthropic (Mienis & Rittner, 2010; Salgado, Alabau & Meseguer, 2010; Peltanová *et al.*, 2012; Mumladze, 2013). According to Lubell (2004a, b), large edible snails were actively spread by prehistoric humans in the Mediterranean. It is also very likely that *H. lucorum* was introduced by humans in the Caucasian region in the mid-Holocene or even earlier.

In contrast to *H. lucorum*, *H. buchii* is a typical Caucasian (endemic) species mainly inhabiting damp broadleaved (mainly beech) mountain forests between the Black and Caspian Seas (excluding the northwestern Georgian mountains). It also occurs (but is not common) in some subalpine and anthropogenic areas (Mumladze, Tarkhishvili & Murtskhaladze, 2013

and this study). The two species are distributed sympatrically at the country scale and the boundaries of their distributional ranges almost completely overlap within Georgia (Fig. 1). Several years of personal observation showed that in Georgia *H. lucorum* completely avoided natural habitats, which were mostly selected by other large helicoid species [*H. buchii*, *H. goderdziana* Mumladze, Tarkhishvili & Pokryszko, 2008, *H. albescens* Rossmässler, 1839, *Lindholmia nordmanni* (Mousson, 1854) and *Caucasotachea calligera* (Dubois de Montpéroux, 1840)]. The most intriguing fact in the distribution of the two focal *Helix* species in Georgia is that they never co-occur (i.e. they show a parapatric spatial pattern within sites), whereas for example *C. calligera* is frequently found together with either *Helix* species. A similar distribution pattern of another *Helix* pair (*H. pomatia* Linnaeus, 1758 and *H. lutescens* Rossmässler, 1837) without co-occurrence was reported from Poland, although without an attempt to explain the underlying mechanisms (Koralewska-Batura, 1999). The pattern described above raises a question of the possible role of interspecific interactions and species-specific ecological requirements as possible drivers of the distribution of *Helix* species in Georgia. It is well documented that the distribution of snails is much dependent on environmental factors, whereas the role or even existence of competitive relationships as a factor affecting



**Figure 1.** Map showing the study area with the sampling points for the analysed species. Abbreviations: *a*, Lake Tsodoreti; *b*, Ananuri (see Discussion for details).

snail species distribution is questionable (for review see Cameron, 2013).

Ecological niche modelling (ENM) is increasingly used to characterize species distribution patterns (Guisan & Zimmermann, 2000). In general, ENM generates the probabilistic distribution of a given species by constructing the distribution of the species-specific suitable multidimensional niche space as defined by the input variables. ENM can be useful in delimiting the species-specific ecological requirements and finding other potentially important factors (such as interspecific interaction) that shape the species' distribution (Soberon, 2005; Tarkhnishvili *et al.*, 2010; Lawing, Meik & Polly, 2012). The Georgian *Helix* species are almost equal in size (more than 40 mm in shell diameter) and there are no known differences in their ecological requirements (particularly food and space requirements, and life-history characteristics), which might result in different use of environmental resources (as in an example provided by Cameron, 1978). This suggests that there may be strong interspecific competition between these congeners, which makes them avoid co-existence in the same environmental patches. Alternatively, the ecological requirements may be different enough to provide complete separation of the distributional ranges. If the former is true then ENM should produce highly similar distribution patterns for both species; if the latter is the case, the result should be the opposite (i.e. modelled potential distributions alone should be sufficient to explain the observed pattern without considering interspecific interactions). *Caucasotachea calligera* often co-occurs with either *Helix* species. Hence the prediction is that competition between *C. calligera* and *Helix* species is not an important driver of their distribution and the ENM differences between them should be smaller than those between the *Helix* species. Here, I test these alternatives by constructing and comparing ecological niche distribution models for the two *Helix* species and *C. calligera*.

## MATERIAL AND METHODS

### Distributional data

In order to investigate the distribution pattern of the two *Helix* species in Georgia, I used the distributional data for both species recorded by myself during the past 7 years (Fig. 1; Supplementary

Material: Appendix S1). In constructing ENMs, I used localities for which exact geographic coordinates were available: 49, 36 and 37 localities for *H. lucorum*, *H. buchii* and *C. calligera*, respectively.

### Environmental variables

The distribution of snail species is strongly affected by climate, vegetation and soil types (Dunk, Zielinski & Preisler, 2004; Horsák, 2006). Hence it might be important to use these variables in order to ensure the accuracy of ENM approach. Unfortunately, information about those soil variables important for snails (soil type, calcium content, pH etc.) is either unavailable or at too coarse a scale in Georgia. Instead I used available climatic variables, vegetation data, land cover and geographical information, all of them with 1 km<sup>2</sup> resolution. I used 19 bioclimatic variables presenting biologically meaningful climatic information, which was derived by the combinations of monthly temperature and rainfall (data available at: <http://www.worldclim.org/>) (Hijmans *et al.*, 2005). The composition of vegetation and its density are strongly dependent on the climate (Woodward, 1987; Stephenson, 1990), however the distribution of vegetation is also affected by temporal factors, such as harvesting, grazing and other anthropogenic and nonanthropogenic drivers (Chuine & Beaubien, 2001; Palmer *et al.*, 2005). For this reason I also included vegetation data with the climate variables in the model. SPOT Vegetation ten-daily synthesis data (available at <http://free.vgt.vito.be/>) were used to extract monthly normalized difference vegetation indices (NDVI) as a proxy of monthly vegetation cover. I used ten-daily time series data from 2004 to 2010 to generate average monthly NDVI grids (12 variables in total) using the free extraction software VGT Extract v. 2.0.1 available with the data. Together with the climate and vegetation data, physical geographical variables such as elevation, aspect and slope (the last two derived from the elevation data using Arc GIS v. 9.3; ESRI, Redlands, CA) were included in the model. Besides these continuous variables, I also included land cover categories (17 classes) derived from MODIS land cover data (MCD12Q1; Friedl *et al.*, 2002, 2010). This variable describes different types of land cover such as forest, grassland, cropland, settlements and others and can be useful in understanding of species distribution (for details of land cover

categories see Supplementary Material: Appendix S2). In total 34 continuous and one categorical variable were used to build ENMs (Table 1).

*Distribution modelling*

There are many algorithms available to model the potential distribution of species (Elith *et al.*, 2006). The choice of modelling techniques depends on several factors. When true absence localities within the range of target species are hard to define, algorithms relying solely on presence data are the best choice (Pearson, 2010). Among the presence-only modelling techniques, the maximum entropy (Maxent) approach (Phillips, Dudík & Schapire, 2004) seems to outperform others (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Pearson *et al.*, 2007; Tognelli *et al.*, 2009; Gastón & García-Viñas, 2011; Broennimann *et al.*, 2012). This uses information contained in the presence localities to compare those points with background data (randomly selected points sometimes called pseudo-absence localities) and calculates percentage contribution of each input variable. There are several advantages to Maxent, which is why it is frequently

chosen. One of the most important is its powerful capability to analyse piecewise linear responses of species to the explanatory variable ('hinge' feature) (Elith *et al.*, 2011). In all modelling experiments I used Maxent with the 'hinge' function to calculate a logistic model that returns probabilities of occurrence for each grid cell ranging from 0 to 1. For each run 25% of occurrences were randomly selected as test data and the remaining as training. I also used the jack-knife statistic (built-in option of Maxent software) to evaluate variable importance for each model. The model performance was assessed using the area under the ROC (receiver operating character) curve (AUC) (Swets, 1988; Fielding & Bell, 1997). Models with AUC value more than 0.75 were regarded as good.

In spite of the fact that Maxent algorithm is one of the most robust methods against multi co-linearity and high dimensionality in input data (Elith *et al.*, 2011), prior to the final modelling I performed filtering of highly correlated variables as suggested by Wisz *et al.* (2013). For that I extracted values for all the localities using ArcGIS and then subjected them to pairwise linear correlation (SPSS Inc., Chicago, IL, USA) to identify highly correlated pairs ( $R^2 > 0.75$ ). One of the partner variables of

**Table 1.** Environmental variables used in the Maxent modelling and their percent contributions for building final models.

Variable	Description	Percentage contribution		
		<i>Helix buchii</i>	<i>Helix lucorum</i>	<i>Caucasotachea calligera</i>
<b>bio1</b>	Annual mean temperature	3.4	3.6	4.6
<b>bio2</b>	Mean diurnal range (monthly mean, T° max -T° min)	5.4	4.6	0
bio3	Isothermality (bio2/bio7) × 100	–	–	–
<b>bio4</b>	Temperature seasonality (SD × 100)	19.4	4	2.9
bio5	Maximum temperature of warmest month	–	–	–
<b>bio6</b>	Minimum temperature of coldest month	0	0	0
bio7	Temperature annual range (bio5-bio6)	–	–	–
bio8	Mean temperature of wettest quarter	–	–	–
<b>bio9</b>	Mean temperature of driest quarter	0	9.8	2.7
<b>bio10</b>	Mean temperature of warmest quarter	2.4	16.8	0
<b>bio11</b>	Mean temperature of coldest quarter	0	0	0
bio12	Annual precipitation	–	–	–
bio13	Precipitation of wettest month	–	–	–
bio14	Precipitation of driest month	–	–	–
bio15	Precipitation seasonality (coefficient of variation)	–	–	–
bio16	Precipitation of wettest quarter	–	–	–
bio17	Precipitation of driest quarter	–	–	–
<b>bio18</b>	Precipitation of warmest quarter	4.1	2.5	1.5
bio19	Precipitation of coldest quarter	–	–	–
ndvi1	Normalized Difference Vegetation Index: for January	–	–	–
ndvi2	for February	–	–	–
ndvi3	for March	–	–	–
ndvi4	for April	–	–	–
<b>ndvi5</b>	for May	20	0.5	46.5
<b>ndvi6</b>	for June	20.9	0	1.6
<b>ndvi7</b>	for July	3.9	0.9	0.1
<b>ndvi8</b>	for August	0	27.8	2.1
ndvi9	for September	–	–	–
ndvi10	for October	–	–	–
ndvi11	for November	–	–	–
ndvi12	for December	–	–	–
<b>landcover</b>	Land cover categories	19	12.2	3.2
<b>alt</b>	Altitude	0	14.2	22.2
<b>Slope</b>	Slope	1.5	2.9	12.6
Aspect	Aspect	–	–	–

Bold variables (left column) were used in final modelling as the most informative and least correlated variables (see text for details).

each highly correlated pair was removed by judging which variable could be more important over its partner, based on practical knowledge. In order to make two niche models comparable it is essential to generate models based on the same input data. For this reason I removed only variables which were unimportant for both species. In this manner, I reduced the number of variables to 15, which were then subjected to final modelling in Maxent (Table 1).

Computation of the overlap between the two distribution models based on Maxent output can be done either by direct calculation of probability values containing ASCII grids or by applying thresholds to derive presence-absence potential distribution maps. In the first case I used ENMTools v. 3.1 (Warren, Glor & Turelli, 2010), which calculates niche overlap using Hellinger's metric— $I$  (Warren *et al.*, 2010). This is simply a similarity measure that is calculated after normalizing each model, so that the sum of all the grid cell values in each model is 1. After calculating niche (model) overlap, I performed the niche identity test (ENMTools): the occurrence data of both species were merged and then randomly divided into two new subsets (the same number of occurrence points for each species) 100 times. For each replicate, Maxent runs were performed and overlap values were calculated. As the Maxent model produces no zero probabilities (but close to zero when suitability is very low) for each grid cell, the  $I$  index may be somewhat overestimated. To avoid this difficulty, I applied the maximum training sensitivity plus specificity threshold rule (Jiménez-Valverde & Lobo, 2007) to produce presence-absence suitability models and then simply calculated the overlap percentage using ArcGIS (i.e.  $\text{overlap} = a/(b + c - a)$  where  $a$  = number of overlapping pixels,  $b$  = number of presence pixels of the first species and  $c$  = number of presence pixels of the second species).

## RESULTS

In general Maxent performed very well for all species (AUC = 0.82, SD = 0.055 for *H. buchii*; AUC = 0.94, SD = 0.02 for *H. lucorum* and AUC = 0.9, SD = 0.07 for *C. calligera*). Overall, the models correctly predicted all known occurrences for both *Helix* species. In particular, the western part of the Great Caucasus where *H. buchii* is absent was also excluded by Maxent, as well as the Colchis lowland and the eastern Georgian dry belt. For *H. lucorum*, the west Georgian humid lowlands and most of the high montane forests were also correctly excluded by the model (Fig. 2). The high-likelihood area for *C. calligera* was somewhat smaller than expected. Specifically, all the high mountain regions were excluded from the model. Compared with either *Helix*

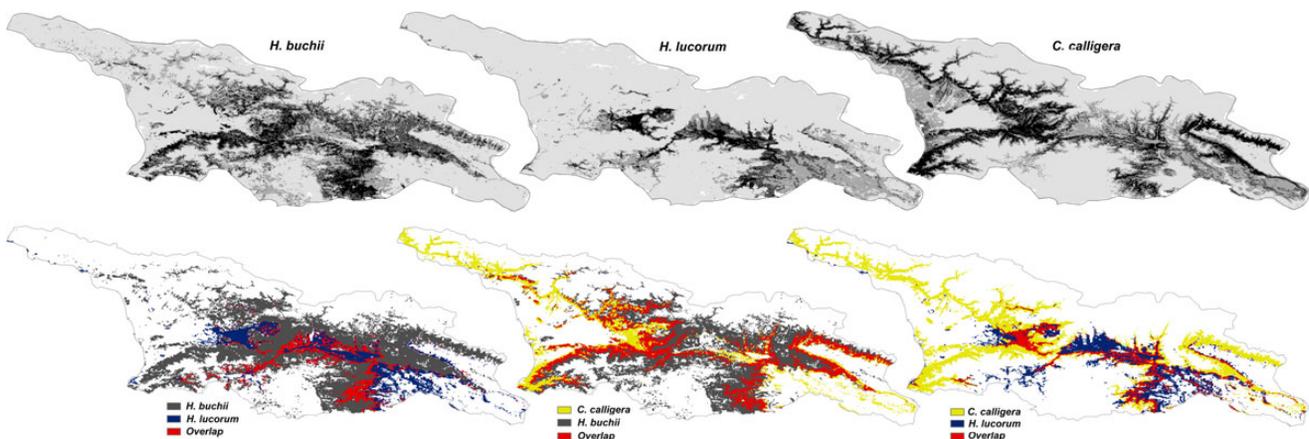
species, *C. calligera* is more widespread. However it is not known if high mountain forests are suitable for its occurrence (Neubert & Bank, 2006). Indeed there are no records of *C. calligera* from altitudes higher than 1600 m. The Colchis lowland where *C. calligera* does occur (but with very low densities) is predicted as low-likelihood.

The importance of variables differed among species. For *H. buchii*, elevation, the presence of forest (land cover categories 5 and 8; Supplementary Material: Appendix S2) and vegetation density in August were the most important variables and determined 60% of its distribution. The same factors were also informative for the distribution of *H. lucorum* (68% in total), but in contrast to *H. buchii* categories 8 and 13 (savannah and urban areas respectively) had high loadings (Table 1). For both species elevation made the greatest contribution; both showed a similar response along that variable. Altitude and slope were the most important determinants for the distribution of *C. calligera* (89% contribution). With increasing altitude and slope the probability of occurrence of this species decreased (as demonstrated by the response curves derived by Maxent; results not shown).

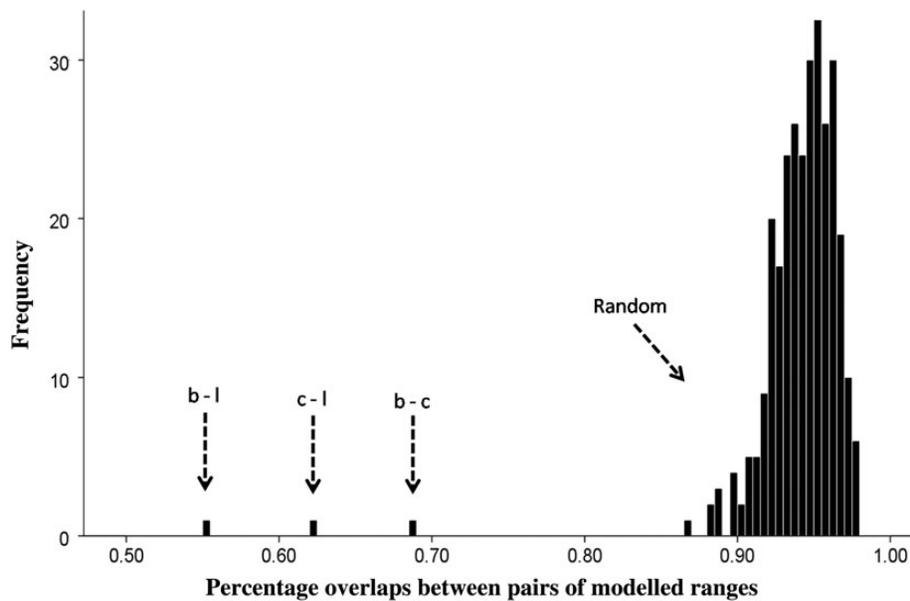
The distinctness of ecological niches between all the pairs was significant ( $P < 0.01$  after 300 randomized replications (Fig. 3)). However, the overlap between the predicted ranges of *Helix* species calculated using raw output (i.e. each cell containing probability values) showed that Hellinger's similarity measure  $I = 55\%$  whereas the overlap between the presence-absence models was much smaller (15%). The overlap between the models of *C. calligera* and *Helix* species was higher (*C. calligera* and *H. lucorum* = 62%; *C. calligera* and *H. buchii* = 69%). The overlap calculated for the presence-absence maps was 36% between *H. buchii* and *C. calligera*, and 21% between *H. lucorum* and *C. calligera* (Fig. 2). These statistics indicate that the suitable niches for all the pairs differed significantly from each other, but there were no absolute differences and sympatric co-occurrence was expected in the contact zones.

## DISCUSSION

The concept of a species' niche used frequently in modern ecology is simpler than the concept as originally defined (Hutchinson, 1957, 1978). Species distribution modelling, widely used in modern ecology, is entirely based on the simplified niche concept as determined by the limited number of environmental factors alone. However, the species' actual distribution (realized niche) is often strongly affected by biotic interactions (Chase & Leibold, 2003; Bascompte, 2009; van Dam, 2009) and dispersal limitations (Allouche *et al.*, 2008; Tarkhishvili, Gavashelishvili & Mumladze, 2012). Hence, modelling the distribution of the realized niche



**Figure 2.** Ecological niche models generated by Maxent algorithm. Top maps represent Maxent probability distributions for *Helix buchii*, *H. lucorum* and *Causasotachea calligera* and bottom maps represent overlapping areas for all three pairs.



**Figure 3.** Histogram showing the distribution of the overlap amounts between the predicted ecological niche ranges: b-l, overlap between *Helix buchii* and *H. lucorum*, c-l, between *Caucasotachea calligera* and *H. lucorum*, b-c, between *H. buchii* and *C. calligera*. The right panel of the graph represents the distribution of range overlaps generated after 300 randomizations.

requires incorporation of such factors as well (Araújo & Luoto, 2007; Kissling *et al.*, 2012; Wisz *et al.*, 2013). In contrast, the distribution pattern generated based only on environmental variables refers to the potentially inhabitable areas where a particular set of environmental conditions is met (Miller, 2010; Pearson, 2010). When two closely related species have similar ecological requirements and are sympatric, there is an expectation of competitive relationships; when the ecological niches are distinct, no competition is expected. This argument, however, has an element of circularity. The distinctness of ecological niches can probably be a function of competitive relationships as well (Whittaker, Levin & Root, 1973). Since the modelled distributions represent the potentially inhabitable areas based on environmental requirements, this kind of analysis can be regarded as a useful way to test whether species have similar environmental requirements when they do not influence each other.

The distribution modelling results for *H. lucorum* and *H. buchii* show that their ecological niches are significantly different from the null expectation. There are also significant differences in ecological niches of the remaining pairs, *H. lucorum* vs *C. calligera* and *C. calligera* vs *H. buchii*. Apart from these significant differences, there is also some overlap between all three pairs, meaning that theoretically they are able to live in sympatry in some areas. This prediction is true for *C. calligera*, which co-exists with both *Helix* species in many areas, but this is not the case for *H. buchii* and *H. lucorum*. Why do they not co-occur?

In order to answer this question some additional information should be considered. First, the pattern described above could be taken as evidence of existence of some other limiting factors (e.g. competition) that affect the distribution of *H. lucorum* and *H. buchii* rather than simple differences in their ecological niches. Indeed, if no such limiting factors exist than all three species are expected to co-occur in contact zones, which is true in the case of *C. calligera*. However this species is more distinct phylogenetically than the congeneric *Helix* are from each other, so there might be ecologically differentiated life-history strategies or other means of limiting similarity by which they avoid competitive relationship in the same habitat patch (Abrams, 1983). In spite of the fact that the ecological niches of *H. buchii* and *H. lucorum* are significantly different, the distinctness of their

ecological requirements is not great enough to provide such a pattern. Specifically, in two localities the populations of both *Helix* species are so close to each other (a few metres only between the population edges) that there is no distinctness in environmental conditions. The first of these localities is situated near Lake Tsodoreti (8 km west of Tbilisi). There is a road and a small hill above the lake; the southern slope of the hill is occupied by both species of *Helix*. However *H. lucorum* occupies areas along the road and *H. buchii* is found just above the population of *H. lucorum*. Another locality is around Ananuri village where both *Helix* have mosaic spatial distributions without overlap (Fig. 1). Hence the closeness of the populations is in accordance with the predictions of the model and it is clear that something other than ecological niche differentiation is preventing syntopic coexistence of these two species.

This study is based on environmental variables with resolution of *c.* 1 km<sup>2</sup>. Such a spatial scale may not be sufficient to define accurately the ecological niches for medium-sized terrestrial snails. One may argue that microhabitat specialization rather than competition can drive parapatric distributions at a local scale. Considering that both the studied *Helix* species are generalist feeders, that they reproduce at the same time (from early to late spring usually) and use soil or above-ground shelters for aestivation (personal observation), it is very difficult to explain the above-mentioned cases by microhabitat specialization alone. Obviously, it is impossible to assume strong interspecific competition with confidence; however it seems that competition is driving the distribution of these two *Helix* species in places where populations are adjacent. In Georgia *H. lucorum* is distributed almost everywhere in anthropogenic landscapes and there are no recorded occurrences in truly natural forests or grasslands (the distribution of the species is one of the best studied in Georgia; Lezhava, 1973; Mumladze, 2013). Such a close association with anthropogenic habitats may be the result of predators such as large carabid beetles (e.g. *Carabus caucasicus*), which are widespread in natural habitats in the Caucasus and are normally scarce in anthropogenic areas (Niemelä *et al.*, 2002). This idea is interesting in view of the historical distribution of *H. lucorum*, which may have arrived in Georgia together with humans in the last several thousand years (Lubell, 2004a,

b). However control of distribution by predators alone is not enough to explain the local distributional patterns in the above cases.

In conclusion, the analysis provided here shows that the distinctness of ecological niches at a larger scale than microhabitat patches cannot be regarded as the main factor in shaping the local spatial pattern for *H. lucorum* and *H. buchii*. Instead, other factors like competition, predation, anthropogenic disturbance etc. seem to play a significant role in limiting the range of both species. In spite of the widespread opinion that competition is an unimportant or a very weak force in structuring terrestrial snail communities (Huntley *et al.*, 2009; Schamp, Horsák & Hájek, 2010), particular cases suggest the opposite picture (Cameron, 1970; Baur & Baur, 1990). In order to fully understand the mechanisms underlying the local pattern of spatial distribution of *Helix* species in Georgia the importance of some potential limiting factors must be tested, rather than examining ecological niche differentiation by means of ENM analyses.

### SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Molluscan Studies* online.

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