



Forest snail faunas from Crimea (Ukraine), an isolated and incomplete Pleistocene refugium

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The land snail faunas of 26 forest sites and two open rocky sites in the Crimean Mountains were sampled in 2011. Of the 40 species found within the forests (about half the known fauna of Crimea as a whole), 28 were species with wide western Palaearctic distributions, and only eight were endemic to Crimea. While there were significant differences in the faunas of different sampling areas, these seemed to be a consequence of ecological differences among them rather than a product of geographical isolation and differentiation. Endemic species were large, and not entirely restricted to forest; known endemics not found in these forests are mainly typical of more open habitats. There is no local radiation of small species living in damp forest litter, as with *Leiostylia* species in the Transcaucasian forest refugium, and families such as the Clausiliidae with many endemic forest species in both Transcaucasia and the Carpathians are sparsely represented. The one endemic clausiliid genus, *Mentissa*, occurs in open as well as in wooded habitats. The present faunas are rather poor considering the soil conditions and climate, and the forests hold widespread species often associated with open habitats elsewhere. While there is evidence that these mountains provided a refuge for many animals and plants during glacial episodes further north, the forest snail fauna suggests that full forest cover did not survive throughout the Pleistocene. Rather, the present fauna contains endemics that survived in other habitats and widespread species with good powers of passive dispersal. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, ••, ••–••.

ADDITIONAL KEYWORDS: climate change – dispersal – geographical distribution – species richness.

INTRODUCTION

Forest land snail faunas in northern Europe are largely composed of immigrant species that spread from more southerly refugia after the last glaciation (Hausdorf & Hennig, 2003; Cameron, 2004; Pokryszko & Cameron, 2005; Cameron, Pokryszko & Horsák, 2010; Cameron *et al.*, 2011). These northern faunas are subsets of those further south (Hausdorf, 2006), although, as with some plants (Kullman, 2002), there appears to be a western bias in the sources of immigrants (Cameron *et al.*, 2010). Most species have wide geographical ranges, and although

local faunas may be rich, they contain most of the species in the relatively impoverished regional faunas. As for other organisms, regional variation within northern Europe reflects the diversity of the southerly refugia extending from the Iberian Peninsula to the Balkans (Birks & Willis, 2008). This array of southerly refuges terminates at the Black Sea. While the Carpathian basin and submontane zone provided forest refugia (Willis & van Andel, 2004; Jankovská & Pokorný, 2008), including several snail species characteristic for interglacials further north (Ložek, 2006), as did parts of Transylvania (Björkman *et al.*, 2002; Tantau *et al.*, 2006; Feurdean *et al.*, 2007), the low coastal areas around the Black Sea from Bulgaria to Crimea were steppe during the last glaciation (Atanassova, 2005). At

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the other end of the Black Sea, however, the ancient forest refugium of Transcaucasia supports a very rich and highly endemic snail fauna, amongst others, in which *in situ* evolution has occurred over millions of years (Sysoev & Schileyko, 2009; Pokryszko *et al.*, 2011; Tarkhnishvili, Gavashelishvili & Mumladze, 2012). Very few forest species with more northerly distributions appear to have spread from this refugium, sealed to the north by steppe vegetation. Even in the Southern Urals to the east all species recorded in forests are also present in north-central Europe (Horsák *et al.*, 2010). There is no specifically Caucasian signal in these northern faunas.

The Crimean Peninsula lies within the *c.* 1200 km distance between the Carpathians and Transcaucasia, rather closer to the western end of the latter. It has been surrounded by steppe vegetation both now and during the last glaciation (Atanassova, 2005), but its southern mountains, up to 1500 m high, induce greater precipitation, and shield their southern slopes from cold northerly winds. These mountains are presently forested, but their vegetation and climate in the last glacial period is somewhat uncertain. The northern flanks of these mountains appear to have held some broadleaved trees in interstadials within the last glacial period, but the extent and permanence of forest cover throughout the pleniglacial is unknown; there are few data for the period of the Last Glacial Maximum between 24 000 and 18 000 years ago (Gerasimenko, 2007; Markova, 2010). The most recent analysis of mammal remains at the Emine-Bair-Khosar Cave (Ridush *et al.*, 2013) suggests that steppe was predominant, but with small forest elements present.

The present land snail fauna of Crimea is thought to comprise between 78 and 83 species, excluding slugs and near-marine species. Recent checklists (Leonov, 2009; Balashov & Gural-Sverlova, 2012) differ over some records, but *c.* 50 species are widespread in Europe, a few others are introduced, and 18–19 are thought to be endemic. A few more have an eastern range not extending west of Romania. Many of the endemics are species typical of rocky steppe. Puzanov (1926) made a pioneering ecological and biogeographical analysis of the fauna, based on his own intensive fieldwork and earlier accounts; he distinguished between the steppe faunas of the north and those of the mountains, and attempted to trace the connections with the faunas of the Caucasus and Europe. Our study set out to examine the richness and composition of Crimean forest snail faunas in the same way. In particular, it sought to examine the extent to which the faunas reflected the existence of forest refugia through the Pleistocene, or were the product of Holocene colonization of a previously unin-

habitable region, and to provide a modern baseline for interpreting subfossil assemblages.

THE STUDY AREA

The northern part of the Crimean peninsula is flat, and mostly in intensive agricultural use. Its natural vegetation is steppe. Along the south-east-facing coast, from Sebastopol in the west to Feodosiia in the east, there are mountains arranged in three parallel ridges. The southernmost ridge, descending steeply to the Black Sea coast, is the highest, with a few summits just above 1500 m. The mountains decrease in height to the east. On and around the summits there are largely open karstic plateaux (yailas) with many small dolines, some of which retain forest cover. While the highest areas are limestone, lower areas often include sandstones and schist. Temperature and precipitation regimes are similar to those of central Europe; rainfall ranges from *c.* 1000 mm in the west to 400 mm to the north of the mountains and to the east, and average annual temperatures are in the range 5–10 °C. January temperatures are generally a few degrees below 0 °C, but slightly higher at sea level on the south-eastern coast.

Forest type varies with altitude and location. Except above *c.* 900 m, forests on slopes facing the sea are mainly pine *Pinus pallasiana*. Further inland, forests on limestone are frequently dominated by beech, with hornbeam, linden, ash, and maples also present. In drier, usually lower, areas oaks dominate. Most forests are managed, and some are subject to casual local coppicing.

Our samples were made in the central part of the mountain chain (Fig. 1); the greatest distance between samples was *c.* 51 km. Nine sampling areas, indicated numerically on Figure 1, were visited covering a range of altitude, rock type, and forest composition:

- 1 Kyzyl Koba: three samples from limestone hills with mixed deciduous forests subject to some disturbance at *c.* 500 m;
- 2 Chatyrdagh: six samples from a karst plateau and its fringes at *c.* 1000 m;
- 3 Bakhchysarai: four samples from mixed deciduous woods on low limestone hills subject to some disturbance at *c.* 250–400 m;
- 4 Senvpnoe: two samples from dry, managed oakwoods on schist and sandstone at *c.* 450 m;
- 5 Canyon south of Sokolyne: two samples from oak and beech forests at *c.* 400 m;
- 6 Ai Petri: two samples from mixed forests on steep limestone slopes at *c.* 1050 m;
- 7 Soviets'ke: three samples from pine forests on steep sea-facing slopes at *c.* 530–650 m;

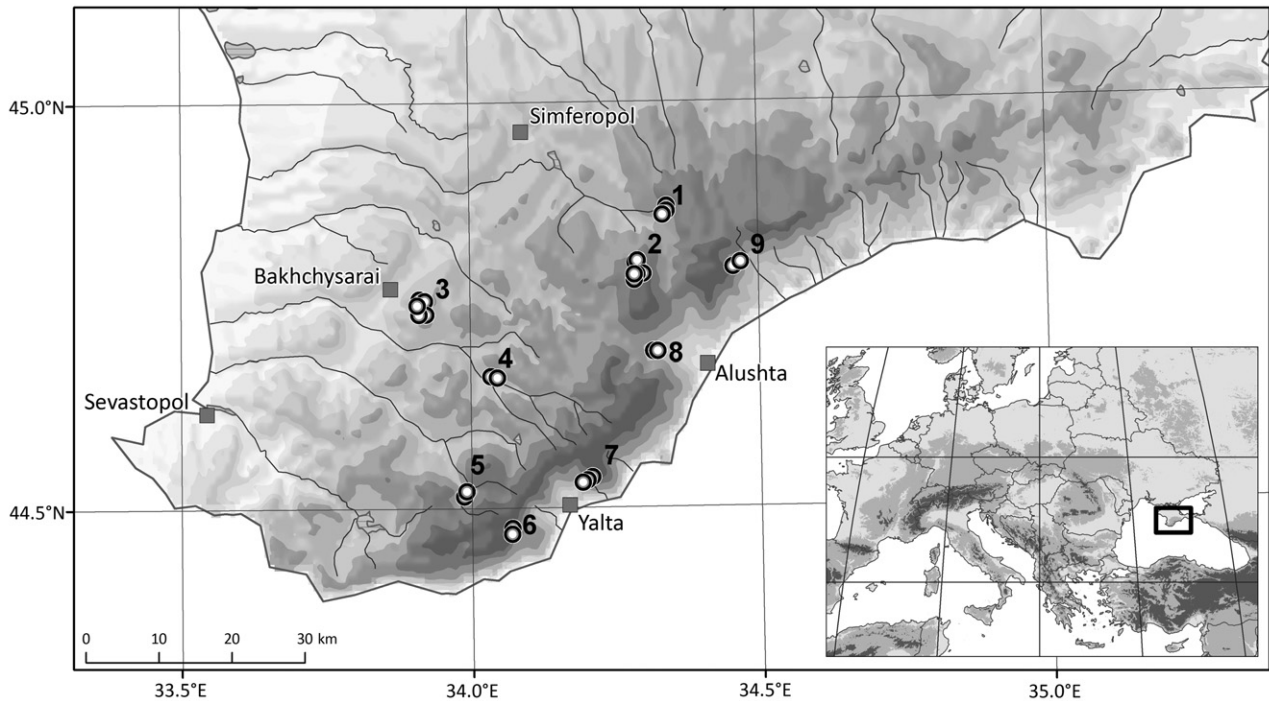


Figure 1. A map of the Crimean Mountains, showing the position of sampling areas. 1, Kyzyl Koba; 2, Chatyrdagh; 3, Bakhchysarai; 4, Senvpnoe; 5, Canyon south of Sokolyne; 6, Ai Petri; 7, Soviets'ke; 8, Rozova; 9, Generals'ke.

8 Rozova: two samples from mixed and disturbed forests with wetter areas than elsewhere at c. 230 m;

9 Generals'ke: three samples from mixed deciduous woods (mainly beech) inland at c. 450 m.

In addition, two samples were made in rocky limestone grassland for comparative purposes, one at Chatyrdagh, the other at Bakhchysarai. Geographical coordinates and other site details are given in Appendix S1 (Table 1).

MATERIAL AND METHODS

At each site, snails from an area of c. 400 m² were collected by hand over about four person hours of searching; in addition about 20 litres of litter was collected and sieved through 10-mm mesh sieves (Cameron & Pokryszko, 2005). Larger specimens were removed from the sieve, and material passing through the sieve was bagged, dried, and then sorted in the laboratory. Slugs were not collected systematically; this method is not appropriate for obtaining a full inventory (Cameron & Pokryszko, 2005). At each site location and altitude were determined by GPS and topographical maps. Certain environmental features were extracted from detailed field notes and coded for statistical analysis. Favourable features were limestone, rocks, steeper slopes, moisture, and

Table 1. Basic data on the faunal composition of forest and open sites

| | Forest | Open |
|------------------------------------|-----------|---------|
| Number of sites | 26 | 2 |
| Total species | 40 | 22 |
| Mean (Median) species per site | 17.7 (18) | 13 |
| Range species per site | 12–23 | 12–14 |
| Mean (Median) individuals per site | 685 (619) | 401 |
| Range individuals per site | 248–1274 | 315–488 |
| Restricted species | 12 | 10 |
| Mean (median) species per site | 5.2 (5) | 6 |
| Range species per site | 3–8 | 6 |
| Widespread species | 28 | 12 |
| Mean (median) species per site | 12.5 (12) | 7 |
| Range species per site | 7–18 | 6–8 |
| Unique species | 26 | 8 |

the presence of dog's mercury *Mercurialis perennis*; unfavourable features were evidence of disturbance and the presence of conifers. Details are given in Appendix S1 (Table 1).

All living and empty but fresh shells were identified to species as far as possible. Very eroded shells and unidentifiable juveniles were excluded. For consistency, nomenclature generally follows Sysoev &

Table 2. Species found in the forest samples, arranged by distribution and frequency of occurrence

| Species | Sites | Areas | Size |
|----------------------------------|-------|-------|------|
| Restricted | | | |
| <i>Monacha fruticola</i> * | 26 | 9 | L |
| <i>Mentissa canalifera</i> * | 24 | 9 | L |
| <i>Oxychilus diaphanellus</i> * | 20 | 7 | L |
| <i>Peristoma rupestre</i> * | 16 | 7 | L |
| <i>Vitrea pygmaea</i> | 15 | 7 | S |
| <i>Mentissa gracilicosta</i> * | 11 | 3 | L |
| <i>Bilania boettgeri</i> * | 9 | 4 | L |
| <i>Oxychilus deilus</i> | 5 | 2 | L |
| <i>Oxychilus iphigenia</i> * | 4 | 4 | L |
| <i>Helix albescens</i> | 2 | 2 | L |
| <i>Oxychilus kobelti</i> | 2 | 1 | L |
| <i>Thoanteus sp.</i> * | 1 | 1 | L |
| Widespread | | | |
| <i>Punctum pygmaeum</i> | 26 | 9 | S |
| <i>Euconulus fulvus</i> | 25 | 9 | S |
| <i>Acanthinula aculeata</i> | 23 | 9 | S |
| <i>Cochlicopa cf. lubricella</i> | 22 | 8 | L |
| <i>Vallonia costata</i> | 22 | 9 | S |
| <i>Merdigera obscura</i> | 22 | 9 | L |
| <i>Vitrea contracta</i> | 21 | 8 | S |
| <i>Vitrina pellucida</i> | 21 | 8 | L |
| <i>Lauria cylindracea</i> | 20 | 8 | S |
| <i>Vertigo pusilla</i> | 19 | 9 | S |
| <i>Aegopinella minor</i> | 17 | 8 | L |
| <i>Truncatellina cylindrica</i> | 10 | 5 | S |
| <i>Pyramidula pusilla</i> | 9 | 5 | S |
| <i>Truncatellina costulata</i> | 8 | 3 | S |
| <i>Cochlodina laminata</i> | 8 | 3 | L |
| <i>Phenacolimax annularis</i> | 8 | 5 | L |
| <i>Carychium tridentatum</i> | 6 | 5 | S |
| <i>Cecilioides acicula</i> | 6 | 2 | S |
| <i>Columella edentula</i> | 5 | 3 | S |
| <i>Truncatellina claustralis</i> | 5 | 3 | S |
| <i>Vertigo alpestris</i> | 4 | 2 | S |
| <i>Sphyradium doliolum</i> | 3 | 2 | S |
| <i>Pupilla triplicata</i> | 3 | 2 | S |
| <i>Discus ruderratus</i> | 3 | 2 | L |
| <i>Aegopinella pura</i> | 3 | 3 | S |
| <i>Cochlicopa lubrica</i> | 2 | 2 | L |
| <i>Vertigo substriata</i> | 2 | 2 | S |
| <i>Helix lucorum</i> | 1 | 1 | L |

The number of sites (maximum 26), of sampling areas (maximum 9) occupied and the size (L, large; S, small) are given for each species (see text). Asterisked species are Crimean endemics.

Schileyko (2009); authorities are given in Appendix S1 (Table 2). For some analyses, we have separated species with a wide western Palaearctic distribution from those either endemic to Crimea or with a pro-

nounced eastern distribution, extending no further west than eastern Romania (indicated in Appendix S1). We have also considered size; following Cameron *et al.* (2010) we rank all species with maximum shell dimension less than 5 mm as small, and the remainder, including semi-slugs, as large.

Among endemic species, specimens in the clausiliid genus *Mentissa* are remarkably variable both among and within populations (Baidashnikov, 2006). We have recognized two of the three species previously recorded in Crimea, *M. gracilicosta* and *M. canalifera*. The third species, *M. velutina* Baidashnikov, 1990 was not found, although it has been reported from Ai Petri (Sysoev & Schileyko, 2009). While those authors recognize a number of subspecies of *M. gracilicosta*, Baidashnikov (2006) regards variation among populations as mainly determined by local environmental conditions. Separation of *M. gracilicosta* and *M. canalifera* was especially hard in some samples from Chatyrdagh. *Thoanteus sp.* from site 21 is probably *T. gibber* (Krynicky, 1833), but was represented only by empty shells (cf. Sysoev & Schileyko, 2009). We have not followed Sysoev & Schileyko (2009) in naming the *Pyramidula* species as *P. rupestris* (Draparnaud, 1801), as Bank (2010) and Balashov & Gural-Sverlova (2012) regard the species recorded from Ukraine as *P. pusilla* (Vallot, 1801). The two species of helicellines (Hygromiidae) found at site 17 were not assigned with certainty to species or genus (probably *Xeropicta*), live adult material for dissection being absent. They are not species found native in western or northern Europe. Representative samples of all species are held in the Museum of Natural History, Wrocław University.

The number of individuals found varied among sites, but in no case was the number less than ten times the number of species, the minimum recommended by Cameron & Pokryszko (2005). There was, however, a positive correlation between numbers of individuals and species among samples (Spearman's coefficient, $r_s = 0.52$, $P < 0.01$). Sampling efficiency was assessed for the four sites with fewest individuals by species accumulation curves. All reached an asymptote of species richness well before the full sample size was reached (data not shown). Assessment by the Chao 1 estimator of missing species (Southwood & Henderson, 2000), following Cameron *et al.* (2010), also indicated that very few species were missed in any site. We have used the observed numbers and occurrences of species without correction in our analyses; most of these involve only the forest series.

We used multidimensional scaling (MDS) to expose the main changes in species composition among the study sites. The abundances of each species were square-root transformed to reduce the influence of

dominant species and Bray–Curtis was selected as a similarity distance between communities. Environmental factors were linearly fitted into the ordination space of the first two dimensions with the function ‘envfit’ in the package ‘vegan’ (Oksanen *et al.*, 2012). MDS was computed in R v. 2.15.2 (R Core Team, 2012) with the package ‘vegan’. Sequential Bonferroni corrections of the significance level were used for multiple comparisons of environmental variables (Holm, 1979). Further analyses of presence and absence data use the Sørensen and Simpson Indices of similarity (Koleff, Gaston & Lennon, 2003) both between sites and between aggregate sampling area faunas. The Simpson Index counteracts the effects of differing richness among sites and sampling areas.

RESULTS

SPECIES RICHNESS AND SPECIES COMPOSITION

Samples were made at 26 forest sites and two in the open. Overall, 48 species were identified among 18 613 individuals. Forty of these species among 17 810 individuals were recorded from the main forest series, and 22 species (803 individuals) in the two open sites. Appendix S1 lists the location, altitude, habitat, and composition of each sample, together with names and authorities for each species. Site locations are shown in Figure 1. Summary data are shown in Table 1, separating the main forest series from the two open sites. Species richness among forest sites is positively correlated with the presence and quantity of rocks ($r_s = 0.602$, $P < 0.01$), which usually also indicated limestone; dog’s mercury was often present at these sites. Sites with many fewer species than expected from this association were either somewhat disturbed with a weak canopy and evidence of grazing pressure (site 4, see Appendix S1), or had a canopy dominated by conifers (site 26). There was no relationship between richness and altitude.

Table 2 lists the species found in forests (authorities in Appendix S1) by status (restricted or widespread) and by size and frequency. Eight species are endemic to Crimea or adjacent areas, and four have a distribution no further west than Romania. The remaining 28 species are widespread in the north-western Palaearctic. There is no difference in occupancy (mean number of sites occupied) between the two groups, and there was also no correlation between the numbers of restricted and widespread species among sites. However, 11 out of 12 restricted species (and all eight of the endemic species) were large, as opposed to nine out of 28 widespread species ($\chi^2 = 11.9$, $P < 0.001$). Sixteen species (40%) were present in more than three-quarters of the sampling areas (five restricted, 11 widespread). Only three

Table 3. Snail faunas in the two open sites, arranged by distribution and occurrence in the forest sites

| | Site 6 | Site 17 | Size |
|----------------------------------|--------|---------|------|
| In forests | | | |
| Restricted | | | |
| <i>Helix albescens</i> | | 1 | L |
| <i>Mentissa gracilicosta</i> * | 1 | | L |
| <i>Monacha fruticola</i> * | 1 | 1 | L |
| <i>Oxychilus diaphanellus</i> * | 1 | | L |
| <i>Peristoma rupestre</i> * | 1 | | L |
| <i>Vitrea pygmaea</i> | 1 | 1 | S |
| Widespread | | | |
| <i>Cecilioides acicula</i> | 1 | 1 | S |
| <i>Cochlicopa cf. lubricella</i> | 1 | | L |
| <i>Helix lucorum</i> | | 1 | L |
| <i>Pupilla triplicata</i> | 1 | | S |
| <i>Pyramidula pusilla</i> | 1 | | S |
| <i>Truncatellina cylindrica</i> | 1 | 1 | S |
| <i>Vallonia costata</i> | | 1 | S |
| <i>Vitrina pellucida</i> | 1 | | L |
| Total | 11 | 7 | |
| Only in open | | | |
| Restricted | | | |
| <i>Brephulopsis cylindrica</i> * | | 1 | L |
| Helicelline a | | 1 | L |
| Helicelline b | | 1 | L |
| <i>Brephulopsis bidens</i> * | 1 | | L |
| Widespread | | | |
| <i>Vallonia pulchella</i> | 1 | | S |
| <i>Oxychilus draparnaudi</i> | | 1 | L |
| <i>Chondrula tridens</i> | | 1 | L |
| <i>Chondrina clienta</i> | 1 | | L |
| Total | 3 | 5 | |

Asterisked species are endemic to Crimea.

species were recorded from just one sampling area: *Helix lucorum* at Bakhchysarai (undoubtedly a product of anthropogenic influence), *Thoanteus* sp. at Ai Petri, and *Oxychilus kobelti* at Rozova.

The two open sites held 22 species in total (Table 3). Eight of these were absent from any of the forest sites. Site 6 (Chatyrdagh) held a fauna differing less from neighbouring forest sites (mean Simpson Index similarity 52%) than did the much lower site 17 (Bakhchysarai: mean Simpson Index similarity 39%). The presence of *Oxychilus draparnaudi* in the latter indicates anthropogenic influence. The two sites had only four species in common (Simpson Index similarity 33%; Sorensen Index similarity 31%). Of the six endemic species recorded in open habitats, four are also found in the forests, the species unique to the open habitats being the pale-shelled enids *Brephulopsis bidens* and *B. cylindrica*. Similarly, the two unique

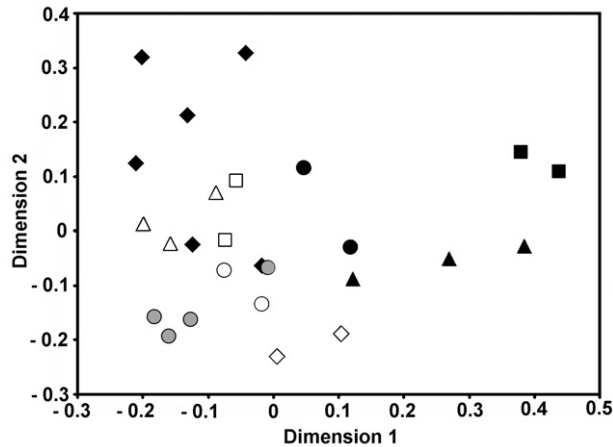


Figure 2. Positions of site faunas along the first two dimensions of the Multidimensional Scaling plot. Filled diamonds, Chatyrdagh; open diamonds, Senvpnoe; filled squares, Rozova; open squares, Canyon; grey circles, Bakhchysarai; filled circles, Ai Petri; open circles, Generals'ke; filled triangles, Soviets'ke; open triangles, Kyzyl Koba.

species with restricted distributions are helicellines typical of open habitats.

PATTERNS OF DIFFERENTIATION

Figure 2 shows the positions of sites on the first two axes of the MDS ordination. These two explain nearly 47% of variation in the data. There is some clustering of sites by sampling area, but, as shown in Table 4, ecological factors (rocks, limestone, and dog's mercury) showed much higher fit to the ordination than position, and these factors are themselves strongly associated; only the first two were significant also after Bonferroni correction (Table 4). It is hard to interpret the weaker geographical correlations by themselves. The first dimension separates samples from Soviets'ke and especially from Rozova from the remainder. These areas were the only ones to hold the two restricted but not endemic species *Oxychilus deilus* and *O. kobelti*, and were the only ones at low altitudes facing the sea. The pattern is not generated by geographical replacement of closely related endemics.

Table 5 shows the overall means, and the mean values within each sampling area for site-by-site values of the Simpson and Sørensen indices of similarity. While the latter represent very small numbers of comparisons it is evident that, with the exception of Chatyrdagh, sites within a sampling area are more alike in their faunas than the overall average. Taking the aggregate fauna of each area (Table 6), the Simpson Index shows that the fauna of Senvpnoe

Table 4. The scores of environmental and geographical variables on the first two dimensions of the Multidimensional Scaling ordination, the fit of each variable onto the ordination (i.e. variation in the factor explained by site scores on the first two MDS axes in the multiple linear regression), and the probability of the result being due to chance, based on 9999 permutations

| | Score 1 | Score 2 | r^2 | P |
|-----------|---------|---------|--------------|------------------------|
| Longitude | 0.155 | 0.988 | 0.181 | 0.1002 ^{n.s.} |
| Latitude | -0.972 | 0.236 | 0.296 | 0.0181* |
| Altitude | -0.364 | 0.931 | 0.286 | 0.0220* |
| Rocks | -0.400 | 0.916 | 0.674 | 0.0001*** |
| Limestone | -0.779 | 0.628 | 0.474 | 0.0012** |

Among nominal factors only the presence or absence of dog's mercury caused a significant difference in position in the two-dimensional space ($P = 0.012$). *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; n.s., not significant; associations significant also at $P = 0.005$ (Bonferroni correction) are in bold.

Table 5. Mean values of the Simpson and Sørensen indices (%) overall and within each sampling area

| | N | Simpson | Sørensen |
|--------------|-----|-------------|-------------|
| Overall | 325 | 75.6 (0.72) | 66.7 (0.63) |
| Chatyrdagh | 15 | 79 | 69 |
| Generals'ke | 1 | 94 | 80 |
| Kyzyl Koba | 3 | 90 | 81 |
| Bakhchysarai | 6 | 88 | 81 |
| Senvpnoe | 1 | 92 | 81 |
| Ai Petri | 1 | 83 | 81 |
| Canyon | 1 | 94 | 77 |
| Soviets'ke | 3 | 89 | 81 |
| Rozova | 1 | 88 | 86 |

Standard errors of the overall means are given in parentheses.

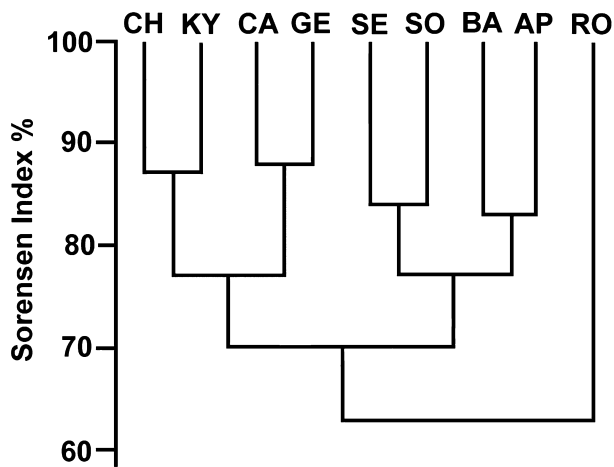
sites is simply a subsample of those found elsewhere: a reduced fauna containing the most frequent species. By contrast, the fauna of Rozova is distinctive, with lower than average relationships to those of other areas. A dendrogram of associations shown by the Sørensen Index (Fig. 3) emphasizes this distinction. Other linkages, however, do not show a consistent pattern in relation to position. Neither the Simpson nor the Sørensen indices using sampling area faunas show any relationship between distance apart and faunal similarity ($R = 0.08$ and 0.07 , respectively).

DISCUSSION

The presence of endemic snail species, accounting for about one-quarter of the recorded Crimean fauna,

Table 6. Values of the Simpson Index of Similarity (%) among all pairs of sampling areas

| | GE | KY | BA | SE | AP | CA | SO | RO |
|--------------|----|----|----|-----|-----|----|----|----|
| Chatyrdagh | 88 | 92 | 75 | 100 | 82 | 88 | 88 | 80 |
| Generals'ke | | 79 | 71 | 93 | 77 | 88 | 76 | 60 |
| Kyzyl Koba | | | 83 | 100 | 86 | 75 | 88 | 70 |
| Bakhchysarai | | | | 100 | 86 | 67 | 88 | 70 |
| Senvpnoe | | | | | 100 | 93 | 93 | 64 |
| Ai Petri | | | | | | 77 | 94 | 65 |
| Canyon | | | | | | | 76 | 60 |
| Soviets'ke | | | | | | | | 76 |
| Rozova | | | | | | | | |

**Figure 3.** A dendrogram of faunal similarities among sampling areas using the Sorensen Index. AP, Ai Petri; BA, Bakhchysarai; CA, Canyon; CH, Chatyrdagh; GE, Generals'ke; KY, Kyzyl Koba; RO, Rozova; SE, Senvpnoe; SO, Soviets'ke.

demonstrates that the peninsula, and in particular the mountains, provided a molluscan refuge through glacial episodes within the Pleistocene. Three out of four enid genera with endemic species are also endemic, as are the single genera of clausiliids and daudebardines with endemic species (Sysoev & Schileyko, 2009; Balashov & Gural-Sverlova, 2012). Other endemic species belong to more widespread genera, but this deeper level of differentiation suggests a prolonged period of survival and isolation. Evidence from mammal remains also shows that the mountains provided a refuge for a diverse fauna within the Pleistocene (Vremir & Ridush, 2005; Markova, 2010; Ridush *et al.*, 2013). The pollen record and lithopedological analysis show a succession of changes associated with warmer interstadials and colder stadials before the last pleniglacial period from *c.* 100 000 to 28 000 BP. The last and most

intense phase of the pleniglacial (24 000–18 000 BP) was characterized by xeric steppe conditions (Gerasimenko, 2007). The reappearance of elements of forest vegetation in the interstadials, including broadleaved trees such as hornbeam, suggests a nearby source. However, with the exception of the cave deposits at Emin-Bair-Khosar at Chatyrdagh (Vremir & Ridush, 2005; Ridush *et al.*, 2013), all Pleistocene data come from the northern side of the mountains at relatively low altitudes, where steppe conditions would be more marked than in the south and at higher altitudes. Nevertheless, Stankovic *et al.* (2011) show that the genetic makeup of red deer *Cervus elephas* populations from Emin-Bair-Khosar was Asian in the last interstadial (*c.* 33 ka BP), but is European in living populations, suggesting a process of local extinction and replacement rather than continuous occupation.

The forest faunas recorded here can be considered in this context. They contained about half of all the species reliably recorded from Crimea. Of the 25 widespread species not found in them, ten are typically wetland species, four are typical of dry open habitats, five are probably introduced, one – *Balea perversa* (Linnaeus, 1758) – is regarded as doubtful by Balashov & Gural-Sverlova (2012), and only five are species commonly found in forests further west. Two of these, the clausiliids *Macrogastra plicatula* (Draparnaud, 1801) and *M. latestriata* (A. Schmidt, 1857), are species typical of central European forests, and their occurrence in Crimea is odd. Sysoev & Schileyko (2009) report *M. plicatula* from Chatyrdagh, but it was not in any of our samples. They do not list *M. latestriata* for Crimea, but it is listed as *M. borealis* (O. Boettger, 1878) without comment in Balashov & Gural-Sverlova (2012). Among more restricted species, 11 recorded endemics are missing from our forest samples (compared with eight found within them). Six of these are enids, and four are *Helicopsis* species (Hygromiidae) typical of dry, open habitats; some are known only from their type

localities. Of the remaining restricted species, three are missing from our forest samples: two helicellines and *Ceciliooides raddei* (O. Boettger, 1879). They are typical of open calcareous habitats.

The majority of species in the forest faunas are widespread, occurring from Great Britain in the west to the Urals in the east (Kerney, Cameron & Jungbluth, 1983; Horsák *et al.*, 2010). The suite of species with eastern affinities is small, and only three of these are found also in the Caucasus. Furthermore, many of the endemic species found are not confined to forests, and it is notable that half of the endemic species in our forest samples also occur in the very limited set of two open sites sampled. The endemic species are all large; there are no local radiations of small species living in damp litter, as with *Leiostyla* in the Caucasus (Sysoev & Schileyko, 2009; Pokryszko *et al.*, 2011). Only two genera of Clausiliidae are present in our samples, one endemic, with a total of three species, contrasted with at least ten genera in the Romanian Carpathian forests and 11 in Georgian forests sampled in a similar manner (Cameron *et al.*, 2011; Pokryszko *et al.*, 2011); even more genera are present in the latter region (Sysoev & Schileyko, 2009). Similarly, these Crimean forests held only one (endemic) hygromiid; Carpathian forests typically hold four or five. Eight of the known Crimean endemics are Enidae (of which only two were recorded in our forests), a family with far more representatives in steppe habitats than in forest (Sysoev & Schileyko, 2009), and a further four are in the xerophilic genus *Helicopsis* (Hygromiidae). In the remaining families with endemics (Clausiliidae, Oxychilidae, and Hygromiidae), the genera represented by endemics are either confined to Crimea (*Mentissa* and *Bilania*) or have many representatives outside forests (*Oxychilus* and *Monacha*). *Monacha* in particular is not a typical forest genus with a majority of species living in open or scrubby Mediterranean habitats (Schütt, 2005).

The evidence thus suggests that although some shade, warmth and moisture beyond what would be expected in steppe conditions persisted in these mountains through the Pleistocene, this did not amount to the persistence of full forest cover over significant areas. Interpretation of mammal remains is concordant with this view (Ridush *et al.*, 2013). The present fauna consists mainly of small, widespread species capable of long-distance passive dispersal (e.g. Cameron *et al.*, 2010; Horsák *et al.*, 2012), together with locally surviving species capable of living under conditions of less than complete forest cover. In particular, the presence of karstic features and limestone screes might facilitate the survival of a few species requiring shade and moisture. These have subsequently been able to occupy existing forests, but can also be found outside them.

There is additional evidence that these isolated forests have snail faunas dominated by post-glacial immigrants. These forest faunas are not especially rich, with similar numbers of species per site to those in Georgia (Pokryszko *et al.*, 2011), and less than in the Romanian Carpathians (Cameron *et al.*, 2011), despite large numbers of individuals and the presence of rocky limestone in many sites, a sharp contrast to the Georgian sites sampled in both features. Both richness and similarity in composition relate to ecological variables. Composition also relates to geographical position, but within this small area there is no indication that similarity is inversely related to distance apart. Some of the geographical effect is caused by the restricted distribution within our samples of species that are not endemic to Crimea (e.g. *Oxychilus deilus* and *O. kobelti*), and we have no evidence of local allopatric replacement of sister species. The endemic *Mentissa* species frequently occur together. We conclude that variation among sites and sampling areas is caused mainly by present environmental factors (including disturbance), with sites in the same sampling area sharing ecological characteristics.

The composition of faunas also shows some peculiarities. There is a suite of species (*Cochlicopa* cf. *lubricella*, *Truncatellina* species, *Pupilla triplicata*, *Phenacolimax annularis*, and *Vallonia costata*) that while not absent from all central European forests are more typical of open or subalpine habitats. Several of these also occur, sometimes at high frequencies, in the forests of the southern Urals (Horsák *et al.*, 2010). These Ural forests have a suite of wetland species not found in our samples, but also two species (*Chondrula tridens* and *Vallonia pulchella*) found only in the open habitat samples from Crimea. Even the richest site in the Ural forests held only 14 species, and most held fewer than ten; Horsák *et al.* (2010) concluded that the forest faunas resembled those of the early Holocene of central Europe, composed of relatively few species with broader ecological tolerances than they show today. The Crimean forests appear to be in an intermediate position, and have an additional source of colonists from relatively temperate open habitats including local ones in which endemic species have evolved. While the issue of competitive exclusion in land snails is a contentious one, with little evidence to support it (Cameron, 2013), it may be relevant that these peripheral forest faunas are also poorer in species than those in those parts of northern Europe closer to sources of colonists, and in particular to colonists originating from forest refugia. Local richness may be constrained by the available species pool. We note that Crimea is isolated not only by distance, but also by the surrounding steppe that has persisted through the Pleistocene (Atanassova,

2005; Gerasimenko, 2007). We can pose some questions: do differences among the faunas of different habitats in the same region relate to the length of time they have been maintained, or to the proximity of sources from the same range of habitats? How has the fauna of the Crimean Mountains changed over the Pleistocene? Shell-bearing deposits are known from the Emine-Bair-Khosar cave that might at least partly answer the latter question.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Appendix S1. Data from: Forest snail faunas from Crimea (Ukraine), an isolated and incomplete Pleistocene refugium.

ARCHIVED DATA

Data deposited in the Dryad repository: doi:10.5061/dryad.q34fp (Cameron, Pokryszko & Horsák, 2013).