INVASION OF A CRIMEAN LAND SNAIL *BREPHULOPSIS CYLINDRICA* INTO PROTECTED RELICT STEPPIC HILLTOPS (TOVTRS) IN WESTERN UKRAINE: A THREAT TO NATIVE BIODIVERSITY?

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Abstract Brephulopsis cylindrica *(Menke 1828), a snail native to the Crimea, has been expanding northward and westward, and has recently reached Western Ukraine. Three adjacent and abundant colonies have been found in the tovtrs (small rocky hilltop areas of protected relic steppic habitat) of the Podilski Tovtry National Nature Park in Western Ukraine. These sites and ten similar sites without* B. cylindrica *were sampled. Most of the snail species that occur in the other ten sites were absent from the samples from the sites with* B. cylindrica*, which have much lower molluscan diversity. It is suggested that* B. cylindrica *is excluding some threatened native snails that have comparable ecological preferences, notably* Helicopsis striata*. Possible mechanisms of competition with native species are discussed. The most likely explanation is that these native snails are displaced from seasonal refuges in rock crevices as a result of the high densities of* B. cylindrica*. The snails in Western Ukrainian populations of* B. cylindrica *are smaller than in populations from the Crimean mountains, but similar in size to populations from the Crimean plains, which may be where they originated.*

Key words *Competition, exclusion, conservation, terrestrial molluscs, grasslands,* Brephulopsis cylindrica

INTRODUCTION

Biological invasions are one of the most significant environmental issues of the 21st century and are known to have major negative consequences for both human enterprise and ecological systems (Pimentel *et al*., 2000). Some non-indigenous species can acclimatise in natural ecosystems far from their original ranges and cause decline in native species, often those that are most threatened, as a result of competition as well as direct predation (Vorburger & Ribi, 1999; Rushton *et al.,* 2000; Cowie, 2001; Ohtaka *et al.,* 2005; Dunn *et al*., 2009; Miller *et al*., 2010; Strauss *et al*., 2012). Studying such cases to understand their mechanisms is important for the development of biodiversity conservation and the control of invasive species. Terrestrial molluscs are especially interesting in this regard as they have low mobility and so may be particularly threatened, but study of their displacement by competing non-carnivorous non-natives has been overlooked (Cowie, 2001; Lydeard *et al.,* 2004; Régnier *et al*., 2009, 2015).

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Brephulopsis cylindrica (Menke 1828) (Stylommatophora: Enidae), a land snail native to the Crimean Peninsula (Ukraine), is now widely distributed in the grasslands of the Black Sea Lowlands and some adjacent regions in Ukraine, Moldova and Russia (Sverlova *et al*., 2006; Vychalkovskaya, 2008; Balashov & Gural-Sverlova, 2012; Balashov *et al.,* 2013b, c), and was first recorded in Central and Western Ukraine in the 1990s (Sverlova *et al.,* 2006). It is one of the commonest and most abundant terrestrial snails in the Crimean Peninsula, where it inhabits open dry habitats, such as steppes and rocky grasslands, feeding mainly on live and dead lichens and plants (Schileyko, 1984; Sverlova *et al*., 2006; Balashov & Baidashnikov, 2013). Outside the Crimea, *B. cylindrica* mostly lives in anthropogenic habitats such as the sides of roads and tracks, lawns and wastelands. It is often spread by people with plants, building materials etc., thus extending its range (Sverlova *et al.,* 2006). Fossil evidence for *B. cylindrica* has not been found outside the Crimea (Kunitsa, 2007), so it is most likely that its expansion to the mainland Eastern Europe took place in the Holocene. The biology of *B. cylindrica* (variability,

reproduction, dispersal, behaviour, parasites, etc.) has been intensively studied in the last 20 years (Kramarenko, 1996, 1997, 2009, 2014; Sverlova *et al.,* 2006; Vychalkovskaya, 2008 and others).

The availability of the current name of this species has been questioned (Welter-Schultes, 2012), but retention of the name was subsequently proposed (Balashov & Welter-Schultes, 2013).

In 2014 colonies of *B. cylindrica* were found by the authors in the relict natural steppe hilltops (tovtrs) of the Podilski Tovtry National Nature Park in the Khmelnytskyi region (Podolian Upland, Western Ukraine). This protected area was created for conservation of the peculiar biodiversity of the Tovtry Ridge, a hilly upland (up to 409m above sea level) formed by reef limestones. Many rare steppe and rock-dwelling species survive here on the small rocky hilltops that are called tovtrs. These hills are mainly surrounded and isolated from each other by cultivated land and settlements. Despite significant malacological studies in recent years (Balashov *et al.,* 2013a), *B. cylindrica* has not previously been found in this area.

Once these colonies had been found, the aim of our investigation was to study the possible threat posed by the non-native *Brephulopsis cylindrica* to the native molluscan biodiversity of the steppes, and in particular to threatened species; also to investigate the possible origin of these colonies.

Material and Methods

The main material was collected in May 2014 in the Podilski Tovtry National Nature Park, near Bila village (Chemerivci district, Khmelnytskyi region of Ukraine), from three separated steppe areas on tovtrs (Fig. 1): site 1 (0.097km^2, Fig. 2) – 48°55'15''N 26°28'22''E, altitude 280m; site 2 (0.068km^2) – 48°55'13''N 26°28'14''E, 290m; and site 3 (0.078km^2) – 48°55'2''N 26°27'59''E, 290m. These three sites are separated by a small river and dirt roads (sites 1 and 2), and by a tarred concrete road (sites 2 and 3). Ten samples of terrestrial molluscs from other similar sites in the Podilski Tovtry National Nature Park have been used for comparison: (site 4 – Samovyta Tovtra near Bila village (48°53'43''N 26°29'21''E, 290m, 30.09.1990, leg. Baidashnikov A.; 18.05.2014, leg. Balashov I.); site 5 – tovtr, further south towards Samovyta (48°53'20''N 26°29'38''E, 280m, 30.09.1990, leg. Baidashnikov A.); site 6 – Chernecki Tovtrs near Bila village (48°53'35''N 26°29'55''E, 290m, 18.05.2014, leg. Vasyliuk A. and Shyriaieva D.); site 7 – Vapnjarki Tovtra near Bila village (48°54'17''N 26°29'23''E, 285m, 18.05.2014, leg. Balashov I., Shyriaieva D. and Vasyliuk A.); site 8 – tovtr between Bila and Cherneche villages 1 (30.09.1990, leg. Baidashnikov A.); site 9 – tovtr between Bila and Cherneche villages 2 (30.09.1990, leg. Baidashnikov A.); site 10 – Pavlova Tovtra near Chorna village (48°58'30''N 26°28'15''E, 320m, 17.05.2014, leg. Balashov I.); site 11 – Vysokyj Kamin Tovtra near Ivahnovci village (49°6'6''N 26°22'35''E, 350m, 17.05.2014, leg. Balashov I., Shyriaieva D. and Vasyliuk A.); site 12 – Jan Tovtra near Zakupne village (49°6'46''N 26°21'18''E, 300m, 17.05.2014, leg. Balashov I., Shyriaieva D. and Vasyliuk A.); site 13 – tovtr near Panivci village (01.07.1990, leg. Baidashnikov A.). Sites 8–13 are situated outside the area shown on the map (fig. 1) on nearby territories to the south and to the east.

Materials from the listed sites are deposited in the Collection of terrestrial molluscs of I. I. Schmalhausen Institute of Zoology (Kiev, Ukraine).

The studied sites were sampled "faunistically" to reveal as many species as possible; no quantitative samples were taken. All sites were sampled for several hours until we were satisfied that no more species would be found. Dr. Baidashnikov sampled his sites in the similar way. On the sites 1–3 it was especially taken as a goal to find any species other than *B. cylindrica*, because of its numerous shells on the ground, therefore this species was mainly ignored during the search.

All these areas, especially sites 1–7, are environmentally very similar: they share comparable steppe grass vegetation of similar structure, no trees, isolated shrubs, large rocks on the tops of the hills, and similar altitude (280–290m).

The 356 specimens of *Brephulopsis cylindrica* (Fig 3) (137 from site 1; 32 from site 2 and 187 from site 3) were collected and processed using standard methods (Schileyko, 1984). The height and width of the adult shells were measured with vernier calipers. In addition, 26 adult shells from the colony in the Poltava region (Central Ukraine)

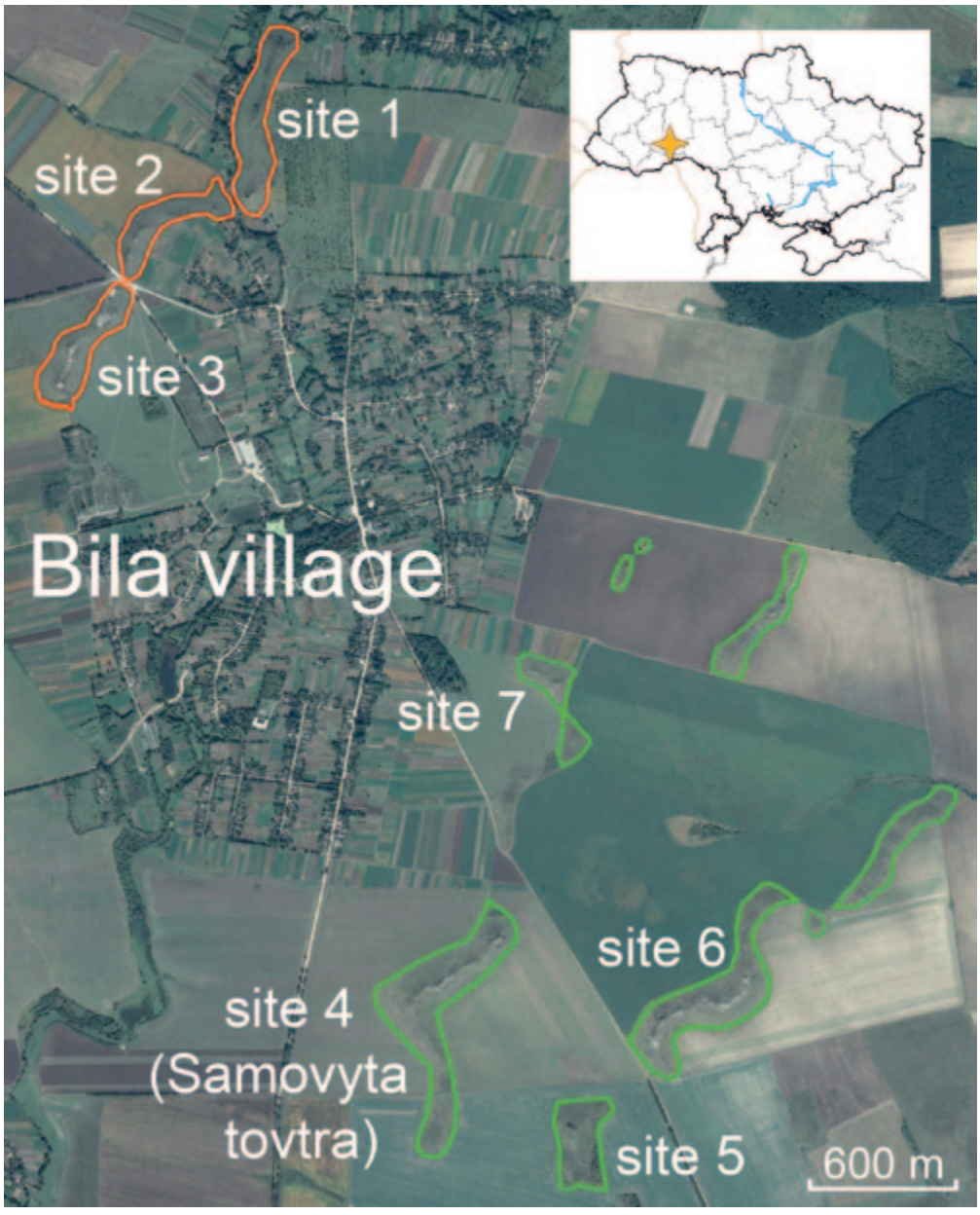

Figure 1 Locations of the sites near Bila village. Red outlines – tovtrs with colonies of *B. cylindrica*; green outlines – other tovtrs.

were measured for this paper (Collection of National Museum of Natural History of National Academy of Sciences of Ukraine, Kiev).

These measurements were compared with previously published data from other populations of *B. cylindrica* (Kramarenko, 1997; Sverlova *et al.*, 2006; Vychalkovskaya, 2008; Kramarenko, 2009) to investigate the origin of the Western Ukraine populations, using the "scattersites" function in Statistica 5.5.

Three methodological approaches were used to test our hypothesis that the invasion of *B. cylindrica* is leading to decreasing diversity of native mollusc species:

1. The incidence-based Chao2 index (Gotelli & Colwell, 2010; Gotelli & Chao, 2013) was used to compare species richness in sites 1–3 (*B. cylindrica* present) and 4–13 (*B. cylindrica* absent) using a presence/absence matrix for the 24 species present in the samples.

2. The one-tail permutation test (Good, 2005) was used to compare the number of species in sites 1–3 (*B. cylindrica* present) and 4–13 (*B. cylindrica* absent).

Figure 2 View of Pervak Tovtra (site 1).

Figure 3 Live *Brephulopsis cylindrica* on a plant and on rock among the lichens (site 3).

3. Non-metric multidimensional scaling (NMDS) was also based on the presence/absence matrix for the 24 species present in the samples. (Borg & Groenen, 2005).

Cochran's Q test (Sokal & Rohlf, 1995) was used to test a hypothesis about non-random formation of the terrestrial molluscs' species composition on the sites with and without *B. cylindrica*.

The programs PAST 1.79 and Random ERT 2.0 were used for statistical calculations

The reproductive anatomy of the snails was investigated to confirm species identification. The

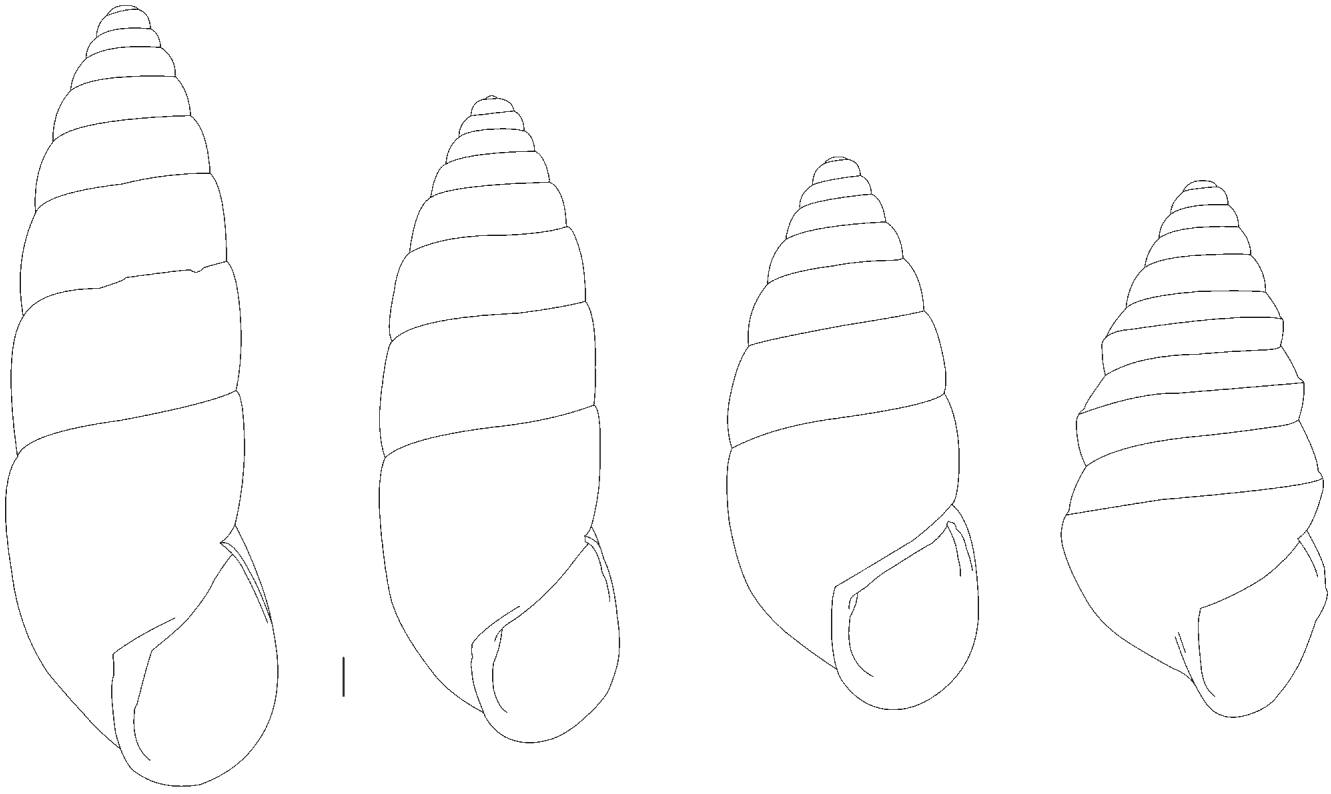

Figure 4 Shells of *Brephulopsis cylindrica* from the vicinity of Bila village.

structure of the penial papilla, penial appendix and epiphallus show that they clearly belong to the genus *Brephulopsis* Lindholm, 1925. However the reproductive system in both the dissected specimens is not quite typical for *B. cylindrica*: section A1 of the appendix and its retractor, which are normally present, are lacking (Fig. 5). This condition has been reported as a within-population variant in *Brephulopsi*s (Schileyko, 1984; Kramarenko, 1996), but has not been previously illustrated.

RESULTS

Twenty-four species of terrestrial molluscs were found in the 13 samples from steppic tovtrs used in this study (Table 1). *Pupilla triplicata* (Studer 1820), *Pupilla bigranata* (Rossmässler 1839), *Chondrina arcadica clienta* (Westerlund 1883) [*C. clienta* was viewed before as a separate species, but is now considered to be a subspecies of *C. arcadica* (Kokshoorn & Gittenberger, 2010)], *Mediterranea inopinata* (Uličný 1887) [until recently generally placed in *Oxychilus* Fitzinger 1833, but now thought to be a separate genus (Balashov, 2014)] and *Helicopsis striata* (Müller 1774) are considered in this region as rare and threatened grassland relics (Balashov *et al*., 2013a; Balashov & Kryvokhyzha 2015). This is the only known population of *Chondrina arcadica,* a rock-dwelling Ukrainian Red Book protected species, in the Ukrainian plains (Balashov *et al*., 2013; the population was checked in 2014). Three species, *Cochlodina orthostoma* (Menke 1830), *Laciniaria plicata* (Draparnaud 1801) and *Morlina glabra* (Rossmässler 1836), are mainly found in forests, and their occurrence in open dry habitats is unusual (Balashov, 2012; Balashov *et al*., 2013a). These species survive on the stepic tovtrs in shady rock crevices.

The colonies of *B. cylindrica* were found in three neighboring sites (1–3) with only a few species of other terrestrial molluscs in low abundance. Two damaged and depigmented fragments of *Laciniaria plicata* were also found. No direct quantitative observations were made, but field observations indicate that the colonies of *B. cylindrica* are of relatively high abundance over the complete extent of sites 1–3 (0.243km^2). The ground is often covered by *B. cylindrica* in these sites. In some parts of the sites there were more than 100 live snails per 1m^2, in other parts only

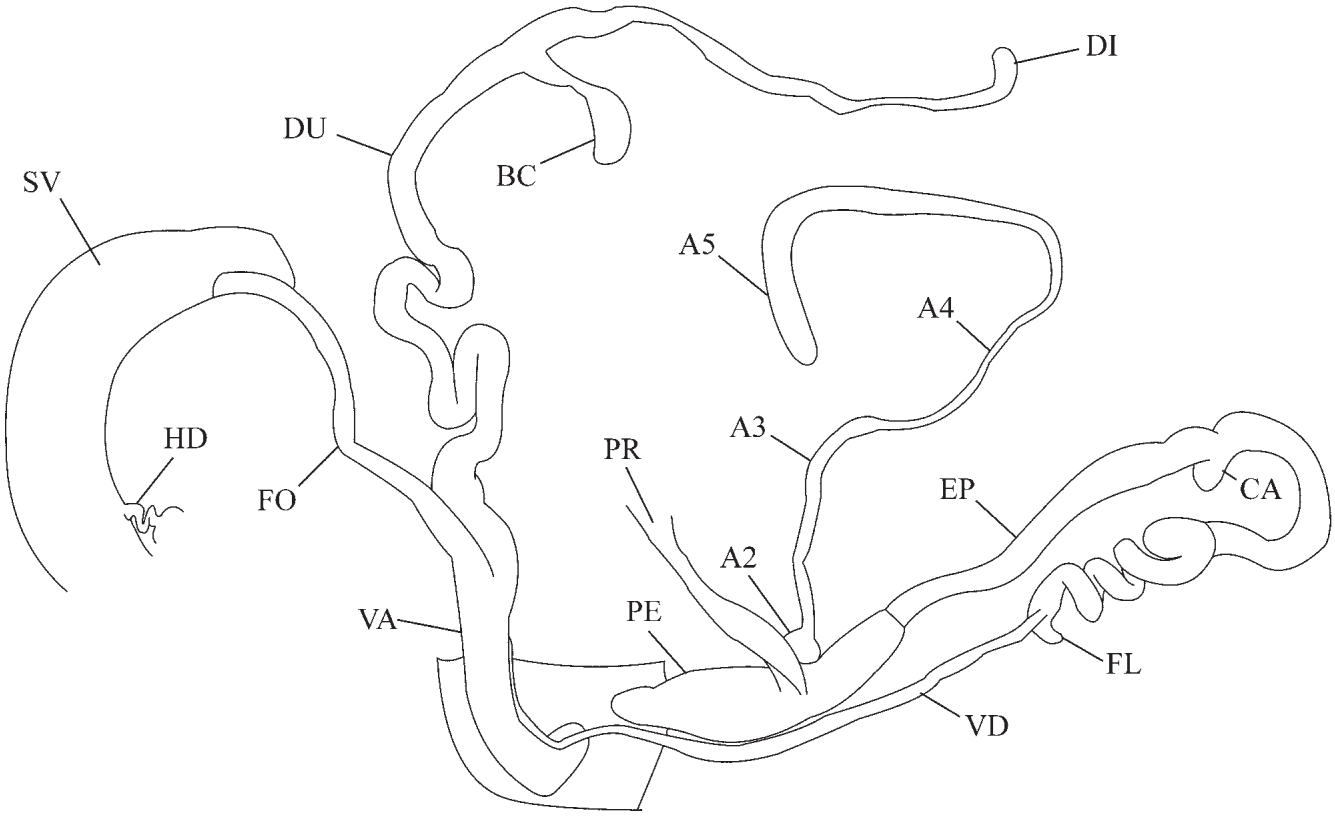

Figure 5 Reproductive system of *Brephulopsis cylindrica* from the vicinity of Bila village. A2–A5 – sections of the penial appendix; BC – reservoir of the bursa copulatrix; CA – caecum; DU – duct of the bursa copulatrix; DI – diverticle of the bursa copulatrix; FL – flagellum; FO – free oviduct; EP – epiphallus; HD – hermaphodite duct; PE – penis; PR – penial retractor; SV – spermoviduct; VA – vagina; VD – vas deferens.

single snails. In the sites where *B. cylindrica* was not present (sites 4–13) the density of the native snails is much lower than for *B. cylindrica* in sites 1–3: in sites 4–13 it usually takes some time to find any snails, in marked contrast to sites 1–3. Even without quantitative assessment, it is clear that the biomass per m^2 of snails (almost all *B. cylindrica*) in the 3 infested sites is very much higher than in the 10 otherwise similar sites without *B. cylindrica*.

Helicopsis striata, a threatened snail that is similar in size to *B. cylindrica* and has similar ecological preferences, was recorded from all studied sites without *B. cylindrica* (4–13), being one of the most abundant snail species in those samples, but was not found from the 3 infested sites (1–3) (table 1). The rock-dwellers *Laciniaria plicata*, *Cochlodina orthostoma* and *Morlina glabra* live together in the same microhabitats on some of the tovtrs without *B. cylindrica* (table 1), where *L. plicata* is the most abundant of the three species. In the sites with *B. cylindrica,* only two damaged depigmented shell fragments of *L. plicata* were found, which suggests its occurrence several years ago and recent extinction.

The species diversity of terrestrial molluscs is very low in the sites with *B. cylindrica* – only 3–4 other species were found. In sites without this invasive species, the number of species found was much higher – up to 15. The Chao2 index of species richness is 4·5±0·7 for sites 1–3 and 21·6±3·8 for sites 4–13.

The permutation test confirms that this difference is significant (p=0.007), supporting the hypothesis that the presence of *B. cylindrica* is associated with low species diversity.

In sites with *B. cylindrica*, only the two or three most enduring native mollusc species remain e.g. *Pupilla muscorum* and *Chondrula tridens* (table 1). Cochran's Q test also shows that the diversity of molluscs in areas without the invader is much higher than in areas with *B. cylindrica* (Q=3.00; df=2; p=0.22 for infested sites and Q=22.25; df=9; $p < 0.01$ for sites without *B. cylindrica*). In a non-metric multidimensional scaling site (Fig 6), the 13 samples are separated into two distinct

Table 1 Presence/absence matrix for terrestrial molluscs in the 13 samples from steppic hilltops (tovtrs) in the "Podilski Tovtry" National Nature Park, Western Ukraine.

	Tovtrs with *B. cylindrica*			Tovtrs without *B. cylindrica*									
Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13
Vallonia costata (Müller 1774)	-	-	-	+	+	+	-	+	-	+	-	-	+
Vallonia pulchella (Müller 1774)	-	+	-	+	+	-	+	+	+	-	+	+	-
Vallonia excentrica Sterki 1893	-	-	-	+	-	-	-	-	-	-	+	-	-
Cochlicopa lubricella (Porro 1838)	-	-	-	+	-	-	-	+	-	+	+	+	-
Pupilla muscorum (Linnaeus 1758)	+	+	+	+	-	+	-	+	+	+	+	-	-
Pupilla triplicata (Studer 1820)	-	-	-	+	-	-	-	-	-	-	-	-	-
Pupilla bigranata (Rossmässler 1839)	-	-	-	+	+	-	+	-	-	-	-	-	-
Chondrina arcadica (Reinhardt 1881)	-	-	-	+	-	-	-	-	-	-	-	-	-
Vertigo pygmaea (Draparnaud 1801)	-	-	-	-	+	-	-	+	+	-	-	-	-
Truncatellina cylindrica (Férussac 1807)	-	-	-	+	+	-	-	+	+	-	+	+	-
Brephulopsis cylindrica (Menke 1828)	+	+	+	-	-	-	-	-	-	-	-	-	-
Chondrula tridens (Müller 1774)	+	+	-	+	-	-	+	-	+	+	-	+	+
Cochlodina laminata (Montagu 1803)	-	-	-	-	-	-	-	-	-	-	-	-	+
Cochlodina orthostoma (Menke 1830)	-	-	-	+	+	+	-	-	-	-	+	-	-
Laciniaria plicata (Draparnaud 1801)	~*	~*	-	+	+	+	-	-	-	-	+	-	-
Morlina glabra (Rossmässler 1836)	-	-	-	+	+	+	-	-	-	-	+	-	-
Mediterranea inopinata (Uličný 1887)	-	-	-	-	-	+	-	-	-	-	-	-	-
Vitrina pellucida (Müller 1774)	-	-	-	+	-	-	-	-	-	-	+	+	-
Arion (Mesarion) sp.	-	-	-	-	-	-	-	-	-	-	+	-	-
Caucasotachea vindobonensis (Pfeiffer, 1828)	-	-	-	-	+	+	-	-	+	-	+	+	+
Helix lutescens Rossmässler 1837	-	-	-	-	-	-	-	-	-	-	-	-	+
Helicopsis striata (Müller 1774)	-	-	-	+	+	+	+	+	+	+	+	+	+
Euomphalia strigella (Draparnaud 1801)	-	-	-	-	-	-	-	-	+	-	-	-	+
Monacha cartusiana (Müller 1774)	-	-	+	-	-	-	-	-	-	-	-	-	-
Species number	**3**	**4**	**3**	**15**	**10**	**8**	**4**	**7**	**8**	**5**	**12**	**7**	**7**

*Only damaged depigmented fragments were found.

clusters along the MSD1 axis. As expected, sites 1–3 make up one cluster, and sites 4–13 the other. The presence of *B. cylindrica* and absence of *H. striata* characterises the first cluster, and the reverse characterises the second cluster (table 1).

The adult shells of *B. cylindrica* in the samples from sites 1–3 (Fig. 4) are 13.5–21.5mm high and 5.3–7.9mm in breadth. The shells are white, sometimes with brown radial stripes. A weak palatal tooth is often present. One of the collected shells is scalariform (Fig. 4, right).

DISCUSSION

The presence of *B*. cylindrica in sites 1–3 appears to be related to a decrease in snail species diversity (Fig. 6). It is known that the number of native terrestrial snail species may be reduced not only as a result of habitat destruction and introduced predators, but also probably as a result of competition with non-native species with similar ecological preferences. Such a situation has been reported for island faunas, however the mechanisms of displacement have not been studied (Cowie, 2001; Cameron *et al*., 2006). In other animal groups species displacement may be caused by displacement from refuges, predation of juveniles or eggs, and diseases or parasites introduced by a more resistant intruder (Park, 1954; Dick & Platvoet, 1996; Vorburger & Ribi, 1999; Rushton *et al.,* 2000; Ohtaka *et al.,* 2005; Dunn *et al.,* 2009; Strauss *et al.,* 2012). It is known that snails that are not normally carnivorous sometimes consume other snails and their eggs, even of their own species (Desbuquois *et al.,* 2000; Ożgo & Bogucki, 2006).

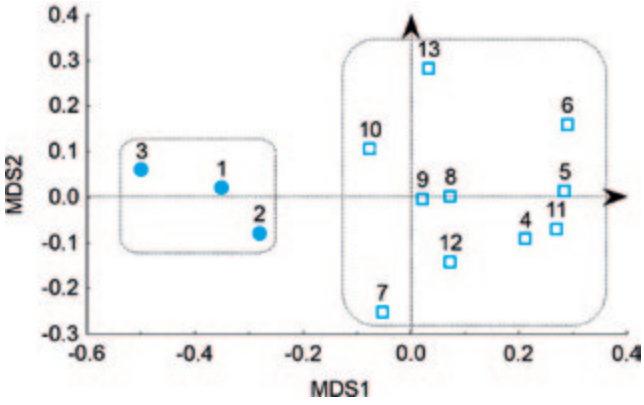

Figure 6 Non-metric dimensional scaling separates the samples of the "Podilski Tovtry" National Nature Park into two clusters.

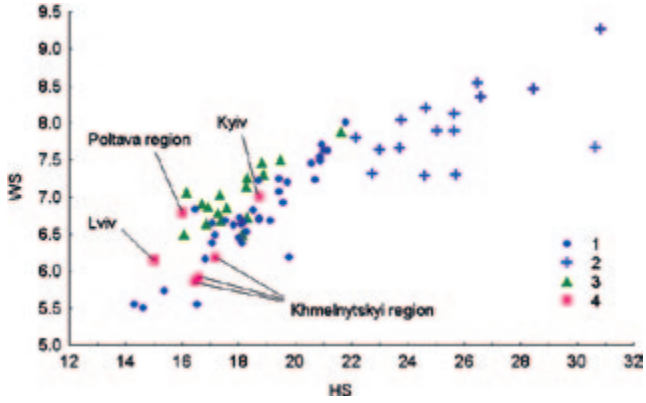

Figure 7 Comparison of the shell width (WS) and shell height (HS) averages (in mm) in populations of *Brephulopsis cylindrica* across its range: 1 – plains of Crimea; 2 – mountains and southern coast of Crimea; 3 – southern mainland Ukraine; 4 – Central and Western Ukraine.

It is therefore possible that *B. cylindrica* can consume the eggs or the juveniles of native snail species and suppress them in this way. Hypothetically the native snails could have been suppressed by some disease or parasite introduced together with *B. cylindrica*. Perhaps in some seasons food resources are not enough to feed all the snails and *B. cylindrica* is more successful due to their density. But it seems to be most likely that the local extinction of some native snail species in the sites with colonies of *B. cylindrica* was caused, first of all, by competition for the space in limited refuges. The survival of land snail species, especially in dry open habitats, depends on the availability of refuges where they hide during droughts and cold weather. For snails in steppe habitats, the most important refuges are cavities among the rocks and in the ground. If the space in such refuges cannot contain all the snails that inhabit the area, some of them will die when conditions are unfavorable. Population densities of *B. cylindrica* are so high that even if the probability of finding a refuge is random, most of the space will be filled by the invasive snails and native snails will be reduced after each unfavorable period until they become extinct. Perhaps some species are more successful competitors for space in refuges than others.

As *B. cylindrica* eats many different types of food including plants, lichens, fungi and their decomposed remains, and its biomass is much higher than that of all the native snails in these habitats, it is possible that it could overgraze and eliminate some scarcer food types in these small steppic islands. It is known that some lichen species may be suppressed by grazing by molluscs (Baur *et al.*, 1994; Fröberg *et al.*, 2006; Asplund & Gauslaa, 2008). There are some relic steppe species in the Podolian Tovtrs that could be of particular concern in this regard, for example the threatened lichens *Squamarina cartilaginea* (With.) and *Solorina bispora* Nyl., both officially protected in Ukraine. However the grazing behaviour of *B. cylindrica* in these habitats has not been studied.

It is very likely that *B. cylindrica* first reached this area at least several years ago, since it occupies all the available area on the 3 infested sites (0.243km^2) even though its active dispersal rate is quite low: no more than 0.42m per day (average 0.15m), 4m per 2 weeks (average 0.45–1.16m in different habitats) and 7.6m in 135 days (average 1.79m) (Kramarenko, 2014). Therefore *B. cylindrica* cannot reach other isolated steppe areas on tovtrs by itself. This species can inhabit much transformed dry grasslands, including some track sides with vegetation. But in the study area such suitable grasslands are much limited and fragmented by the fields with monocultures, shady habitats and unvegetated territories, therefore it is unlikely for *B. cylindrica* to find a direct route through them. However molluscs can occasionally be dispersed by humans and animals (see review in Kramarenko, 2014). The frequency of such dispersals is presumably not high, as it has not happened yet, but it could take place at any time, and should be expected eventually. The relict population of *Chondrina arcadica* on Samovyta Tovtra (site 4) is of particular concern as it is relatively close to sites 1–3 (6km,

Fig. 1). This snail lives among the rocks in the same microhabitats and together with *Laciniaria plicata*, *Cochlodina orthostoma* and *Morlina glabra*, species that appear to have been eliminated from sites 1–3 by *B. cylindrica*.

Another threat is posed by the removal of small rocks from the tovtrs by the citizens of local villages for building material. Many of the fences and some buildings in the area are built of these rocks. Removing rocks reduces the availability of refuges among the rock for snails. On the best preserved of the studied tovtrs, Samovyta, with its population of *Chondrina arcadica* and other rare species, there are many small free-lying rocks covered with mosses and lichens, among which there are numerous cavities. On the other studied tovtrs, most of the loose rocks are larger – too large to be easily removed – with fewer available cavities. It seems likely that the populations of native species on these tovtrs have been reduced by such human activity, which then makes them more vulnerable to the non-native *B. cylindrica.* Perhaps the populations of the native species on the Samovyta Tovtra may be more resistant to an invasion of *B. cylindrica* due to the availability of more larger refuges.

It has been suggested that populations of *B. cylindrica* outside the Crimea have originated from the plains of the Crimea rather than from the Crimean Mountains (Kramarenko, 1997; Sverlova *et al*., 2006; Vychalkovskaya, 2008; Kramarenko, 2009). Comparison of shell width and height averages in populations of *B. cylindrica* across its range shows that shells collected from the steppes of the Khmelnytskyi region are similar to those in the other colonies of *B. cylindrica* in mainland Ukraine and the plains of the Crimea, but much smaller than in the populations in the Crimean Mountains (Fig. 7). This supports the hypothesis that the populations described in this study have originated from the steppes of the Crimea, directly or through other populations.

A few shells of another southern synanthropic species – *Monacha cartusiana*, were also found on site 3, together with numerous *B. cylindrica*. This species is known from several locations in the Podolian Uplands, mainly in settlements, and has been considered as questionably native (Balashov & Gural-Sverlova, 2012; Balashov *et al*., 2013a). As there are no fossil findings of this species in Ukraine (Kunitsa, 2007), it seems likely that *M. cartusiana* also originated from warmer areas and only expanded into mainland Ukraine in the Holocene.

It is not clear exactly how the invasive snails colonized sites 1–3. There are no dumpsites or depots nearby; however Bila village includes a few privately-owned homesteads directly adjacent to sites 1 and 2. Probably snails were brought to these homesteads with building materials or plants from elsewhere and then colonized adjacent steppe areas.

Unfortunately there seems to be no way to completely eliminate these colonies of *B. cylindrica* near Bila without damage to native biodiversity. Natural enemies or collecting by hand can only reduce their number. However, it might be reasonable to use some molluscicide on these 3 sites to prevent further invasion of *B. cylindrica* in the protected steppes in the region; otherwise damage to native biodiversity might be much greater.

The data presented here provide a better understanding of the impact of a biological invasion on native biodiversity. It is a first attempt to analyse in detail the elimination of native terrestrial molluscs by a non-carnivorous species with similar ecological preferences. The possible significance of competition for seasonal refuges in some habitats is proposed for the first time in this important group of organisms.

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