

Shells of the Roman snail are important microhabitats for soil invertebrates

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Received 6 August 2021 | Accepted 7 July 2021

Published online at www.soil-organisms.de 1 December 2021 | Printed version 15 December 2021

DOI 10.25674/so93iss3id167

Abstract

Shells of molluscs from snail farms (heliciculture) are used as food additives or construction material and ecological engineering approaches utilize their potential to assist with ecosystem restoration. Previous studies, for example, highlighted the importance of snail shells as microhabitat for threatened arthropod species with particular focus on wild bees nesting in empty shells. This study focuses on shells of the Roman snail (*Helix pomatia* Linnaeus, 1758) and their value as microhabitat for shell adopters in different dominant vegetation forms and sample periods. In total, 1408 empty shells were placed in areas dominated by one of two vegetation forms (herbaceous vegetation or trees) from February to November 2019 (autumn) or from February to June/July 2020 (summer). All collected shells (N = 618) were sealed at the time of collection, frozen and all content was then analysed with a digital microscope. In total, 91.4% of all collected shells were occupied and the average number of shell adopters was 1.5 time higher in shells collected in summer compared to shells collected in autumn. The number of shell adopters per shell was 1.5 times higher in study areas dominated by herbaceous vegetation compared to study areas dominated by trees. Shell width, but not shell height significantly affected the composition of shell adopter communities. Shells with a larger width were more frequently colonized by another gastropod species [*Discus rotundatus* (O. F. Müller, 1774)] than less wide shells. Shells of the Roman snail provide important multipurpose benefits for a wide range of soil organisms, particularly in habitats that were dominated by herbaceous vegetation and in summer. In autumn, shell adopters included isopods, gastropods and spiders in one subset of shells or Collembola in another subset. The future use of commercially available, empty shells from heliciculture in local restoration projects of open, tree-free areas, holds the potential to support a diverse invertebrate fauna with additional refuge habitats.

Keywords Gastropoda | *Helix pomatia* | shell adopter | shelter | soil animals

1. Introduction

In Italy, heliciculture produces 300g of shells per kilogram edible snails (Forte et al. 2016) providing an example for the high amount of industrial shell production. In aquatic ecosystems, research focuses on how to utilize shells to restore ecosystems (Gutiérrez et al. 2003). In terrestrial ecosystems, invertebrate species may also depend on shells as nesting habitats. At least 56 bee species were recorded to nest in snail shells (Müller et al. 2018), and Potts et al. (2005) highlighted that this

nesting resource plays a crucial role in the assembly of local bee communities. However, experimentally introduced shells are not always accepted by potential shell adopters (Bogusch et al. 2020, Heneberg et al. 2020, Hopfenmüller et al. 2020), indicating that environmental factors and specific preferences may limit colonization and acceptance by shell adopters. Romero et al. (2020) for example observed a co-occurrence pattern between individuals of the bee genus *Rhodanthidium* and the snail species *Sphincterochila candidissima* (Draparnaud, 1801). The authors suggested

that climate and soil conditions determine patterns of shell utilization. Bees are also known to use shell habitats under cold and windy weather conditions, which was also shown for other arthropods with 73% of the variation in shell occupation explained by local weather conditions (Moreno-Rueda et al. 2008). Gess & Gess (1999) observed that sand-filled shells in desert habitats offered additional protection from wind. Our understanding of the determining factors for local colonization of shells across different taxonomic groups is however very limited. Given the wide distribution of terrestrial snails and the potential to utilize snail shells from industrial heliciculture in future biodiversity conservation projects (as for example shown for bees and wasps, Heneberg et al. 2020), this knowledge gap is surprising.

Bogusch et al. (2019) and Heneberg et al. (2020) stated that the shells of the Roman snail (*Helix pomatia* Linnaeus, 1758) are more often used by shell adopters than shells of other terrestrial snail species, which may be a consequence of the relatively large shell size. This pattern makes shells of the Roman snail an ideal model to identify factors that are responsible for local colonization and to study the role of intraspecific variation in shell size for colonization. In this study, we therefore focused on invertebrates colonizing experimentally provided shells of the Roman snail in eight established subpopulations of *H. pomatia* (Tluste et al. 2020). With this study, we aim to understand how shell size, the local dominant vegetation and climatic differences between sample periods affect utilization patterns by shell adopters. We hypothesize that a) larger shells support a higher number of individual shell adopters than smaller shells and are utilized by a higher number of taxonomic groups, b) the composition of shell adopter communities is at least partly determined by the local dominant vegetation and c) warm weather conditions result in higher utilization rates in terms of the number of individuals and number of taxonomic groups in shells compared to colder periods.

2. Materials and methods

2.1 Study area, snail shells & invertebrate identification

The study area is an amenity grassland in the southwest of Cottbus, East Germany and the surrounding borderland with approximately 200 m. After intensive agricultural use, an area of 350 ha was turned into a nature protection area in 1990 (Wollmann 2002). Since then, the management practice has been reduced to mowing once or twice a year depending on grass biomass production.

For this study, 1408 empty shells of *H. pomatia* were ordered from a commercial snail farm (Walter Goller, 72525 Münsingen) for placement in eight previously studied subpopulations (Tluste et al. 2020). This number was based on the commercial availability of shells and is higher than in previously published studies on the use of artificial microhabitats by soil arthropods (e.g. Kolenda et al. 2020). Each provided shell was marked with a small point of gold paint in order to distinguish them from naturally occurring shells in the study area. A subset of 704 shells was placed out in February 2019 and was retrieved in November 2019 (colonization up to ‘autumn’), a second subset of 704 shells was placed out in February 2020 and was retrieved in June/July 2020 (colonization up to ‘summer’). Within those subpopulations, we choose 16 study plots based on two dominant vegetation types identified prior to the placement of empty shells (Tab. S1). Areas were either dominated, (in terms of ground cover) by herbaceous vegetation [mainly *Rubus* sp., *Aegopodium podagraria* (Linnaeus, 1758), *Urtica dioica* (Linnaeus, 1758)] or by deciduous trees without herbaceous vegetation. In order to define the dominant vegetation a wooden frame of 1 m² was used in each study plot and the plant species with the highest coverage was determined as ‘dominant’. The dominant vegetation was identified using Spohn et al. (2008).

Natural colonies of *H. pomatia* were present in all study areas during our experimental provision of empty shells. In each of the 16 study areas, 44 shells were placed in an area of 2 m², with no specific distance or pattern between shells. The study areas showed no signs of frequent disturbance by humans. Only 618 of the 1408 shells could be found. At the end of the respective sample period all shells that were still present (N = 618) were collected, closed with an adhesive tape and stored in a freezer compartment. These shells were later measured (shell height and width) and then opened to study the communities of shell adopters. Most Dermaptera, Gastropoda, Heteroptera, Isopoda, Orthoptera and Pseudoscorpiones were identified to species or genus level. Araneae were only identified to family level due to the fact that individuals were subadult. Coleoptera, Diplopoda and Hymenoptera were identified to family level and Acari and most Collembola were identified to suborder level only, either due to the limited taxonomic expertise or due to the low quality of the samples from shells (dried out or damaged) (Tab. S2). In addition to all observed invertebrate individuals, we also recorded the presence of signs of invertebrate utilization such as spider silk, cocoons, pupae, exuviae and faeces of Gastropoda, Isopoda or Dermaptera (Tab. S3). A high-resolution digital microscope (Keyence VHX-950F) was used to analyse shell content and to determine invertebrate individuals.

2.2 Statistical analysis

We used permutational analyses of variance (PERMANOVA, Anderson 2017) as a distribution-free method for uni- and multivariate analysis of variance models. The subpopulation area (1-8) was defined as random variable, and season of collection of shells (factor 'sample period' with levels: autumn or summer) and dominant vegetation form (factor 'dominant vegetation' with levels: herbaceous or tree) were defined as fixed factors. Shell height and width were included as covariables in all models. All interaction terms that included the random factor were excluded from the models. Permutational analyses of variance were performed based on type III sums of squares with 999 permutations and residuals were permuted under a reduced model as recommended by Anderson (2017). Multivariate taxonomic data of the composition of shell adopter communities was transformed into a resemblance matrix for PERMANOVA based on pairwise Bray-Curtis similarities after adding a dummy variable of 0.1 to account for empty shells. Taxonomic groups with occurrences in fewer than 3 out of 24 observed combinations between subpopulation, sample periods and dominant vegetation were excluded from community analyses. In case of univariate dependent data (e.g. average number of shell adopters per shell) Euclidean distances were calculated between all pairs of shells to construct resemblance matrices. To illustrate results of PERMANOVA models Principle Coordinates Ordinations (PCO) are shown based on the described Bray-Curtis resemblance matrices from multivariate composition data.

3. Results

3.1 Abundance and richness of shell adopter communities

Only 618 of the 1408 originally placed shells could be collected (44% of all shells), of which 8.6% showed no signs of utilization. Shell adopters included 1332 individuals of terrestrial invertebrates (Tab. 1). The number of shell adopters per shell differed significantly between sampling periods ($F_{1,605} = 4.96$, $P = 0.012$) and dominant vegetation ($F_{1,605} = 4.61$, $P = 0.019$). The average number of shell adopters per shell was 1.5 times higher for shells collected in summer compared to autumn with generally high variation between shells (mean \pm SD: 2.5 ± 6.0 vs. 1.7 ± 2.3 ; range 0-98 individuals per shell). The number of shell adopters per shell was 1.5 times higher in study areas dominated by herbs compared to

trees (2.5 ± 5.9 vs. 1.7 ± 2.5). The effect of sampling period on the number of individuals did not significantly depend on the dominant vegetation ($F_{1,605} = 2.52$, $P = 0.107$). Shell height ($F_{1,605} = 0.56$, $P = 0.450$) and shell width ($F_{1,605} = 0.00$, $P = 0.947$) did not affect the number of shell adopters significantly. Only Entomobryomorpha (Collembola) and *Anechura bipunctata* (Fabricius, 1781) (Dermaptera) were found with more than 10 individuals in any individual shell. The average number of observed taxonomic groups per shell (1.4 ± 1.3) did not differ significantly between sampling periods ($F_{1,605} = 2.52$, $P = 0.115$) or dominant vegetation form ($F_{1,605} = 3.45$, $P = 0.067$), with no significant interaction between sampling periods and vegetation form ($F_{1,605} = 3.77$, $P = 0.052$). Shell height affected the number of taxonomic groups positively ($F_{1,605} = 5.75$, $P = 0.018$), with no significant effect of shell width ($F_{1,605} = 0.09$, $P = 0.762$).

Table 1 The number of individuals per major taxonomic group for shell adopter communities in the two sample periods (autumn vs. summer) and dominant vegetation types (Herbs vs. Trees) with N as total number of collected shells.

Taxon	Autumn (N = 279)	Summer (N = 339)	Herbs (N = 354)	Trees (N = 264)
Acari	99	155	203	51
Araneae	26	17	24	19
Chilopoda	1	0	1	0
Coleoptera	7	6	5	8
Collembola	138	298	356	80
Dermaptera	2	69	2	69
Diplopoda	5	18	14	9
Gastropoda	84	77	88	73
Heteroptera	11	4	10	5
Hymenoptera	5	16	8	13
Isopoda	91	188	166	113
Orthoptera	1	0	1	0
Pseudoscorpionida	3	11	13	1
Total	473	859	891	441

3.2 Taxonomic composition of shell adopter communities

The composition of shell adopter communities differed significantly between sampling periods ($F_{1,11} = 2.04$, $P = 0.044$), but not between dominant vegetation forms ($F_{1,11} = 1.37$, $P = 0.222$). The significant effect of sampling period did not depend on the dominant vegetation form (interaction term: $F_{1,11} = 0.39$, $P = 0.914$) and did not result from significant heterogeneity in multivariate dispersion ($F_{1,22} = 1.38$, $P = 0.319$). Shell width ($F_{1,11} = 2.79$, $P = 0.008$), but not shell height ($F_{1,11} = 1.82$, $P = 0.078$)

significantly affected the composition of communities. A subset of shells in subpopulations collected in autumn was characterized by high abundances of Collembola from the orders Symphypleona, Poduromorpha and Entomobryomorpha. A second subset of shell adopter communities collected in subpopulations in autumn and summer was characterized by relatively high numbers of *Porcellio scaber*, Linyphiid spiders and *Cepaea* sp. snails, but low abundances of Oribatid mites (Fig. 1). Only study plots with relatively large average shell width were utilized by the snail species *Discus rotundatus* (O. F. Müller, 1774).

Two species of soil macrofauna were almost exclusively observed in shells collected in summer [*Armadillidium vulgare* (Latreille, 1804)] or in study plots dominated by trees (*Forficula auricularia* Linnaeus, 1758), but were generally not very common in local shell adopter communities (Tab. S2).

In this study, 26% of all snail shells were colonized by isopods, of which 35% of the shells showed signs of aggregation. This aggregation was not only observed between individuals of the same species, but also between individuals of different isopod species aggregating in the same shells. *Porcellio scaber* (Latreille, 1804), *Trachelipus rathkei* (Brandt, 1833) and *Armadillidium vulgare* (Latreille, 1804) were observed to share shells frequently.

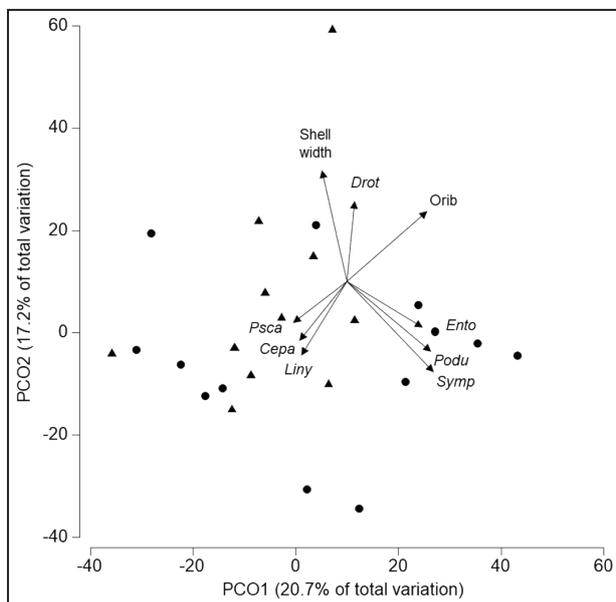


Figure 1. Principle coordinates analysis ordination based on a Bray-Curtis similarity matrix from square-root transformed abundances of 34 taxonomic groups that were at least present in 3 out of 24 study plots in shell adopter communities of 618 Roman snail shells (*H. pomatia*) in autumn (●) and summer (▲). Vectors are superimposed for taxonomic groups with a multiple correlation coefficient > 0.3. **Abbreviations:** Cepa. – *Cepaea* sp., Drot – *Discus rotundatus*, Ento – Entomobryomorpha, Liny – Linyphiidae, Orib – Oribatida, Podu – Poduromorpha, Psca – *Porcellio scaber*, Symp – Symphypleona.

3.2 Indirect signs of shell adopters

The composition of indirect signs of shell utilization differed significantly between sampling periods ($F_{1,11} = 3.64$, $P = 0.017$) and dominant vegetation forms ($F_{1,11} = 2.92$, $P = 0.045$) (Fig. 2). The effect of sampling period on the composition of signs did not significantly depend on the dominant vegetation form in the local habitat ($F_{1,11} = 0.16$, $P = 0.901$). Shell width ($F_{1,11} = 1.10$, $P = 0.354$) and height ($F_{1,11} = 1.39$, $P = 0.2519$) did not affect the composition of signs significantly. A subset of shells collected in autumn was characterized by relatively frequent records of spider silk remains (Fig. 3A) and snail faeces (Fig. 3B). Both these subsets were characterized by an absence of signs for ant nests within the shell (Fig. 2). Isopod faeces (Fig. 3C) were more frequently observed in shells sampled in summer, spider exuviae (Fig. 3D) showed the opposite pattern (Fig. 2).

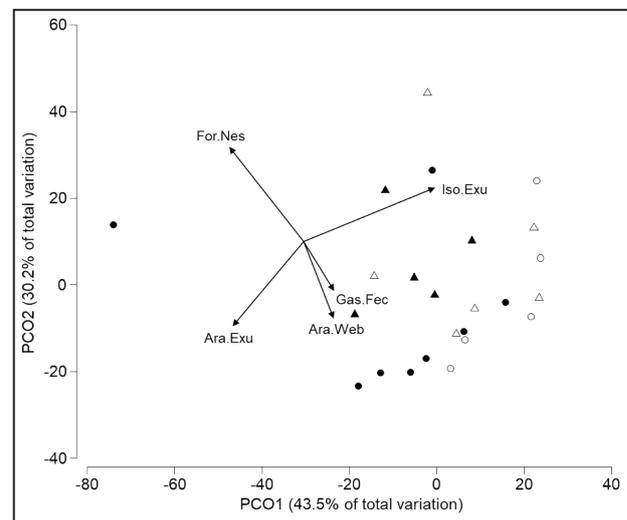


Figure 2. Principle coordinates analysis ordination based on a Bray-Curtis similarity matrix from square-root transformed counts of indirect signs of shell utilization in eight utilization classes of 618 Roman snail shells (*H. pomatia*) in autumn (tree ○ & herb ●) and summer (tree △ and herb ▲). Vectors are superimposed for utilization classes with a multiple correlation coefficient > 0.3. **Abbreviations:** Ara.Exu – Araneae exuvia, Ara.Web – Araneae silk, For.Nes – Formicidae nest, Gas.Fec – Gastropoda faeces, Iso.Exu – Isopoda exuvia.

4. Discussion

Helix pomatia shells were frequently utilized by a range of soil invertebrate taxa in the study area. The benefit of those refuge habitats was particularly high for specific shell adopters including soil meso- (e.g. Acari and Collembola) and macrofauna (e.g. Gastropoda and Isopoda) that was recorded in relatively high numbers.

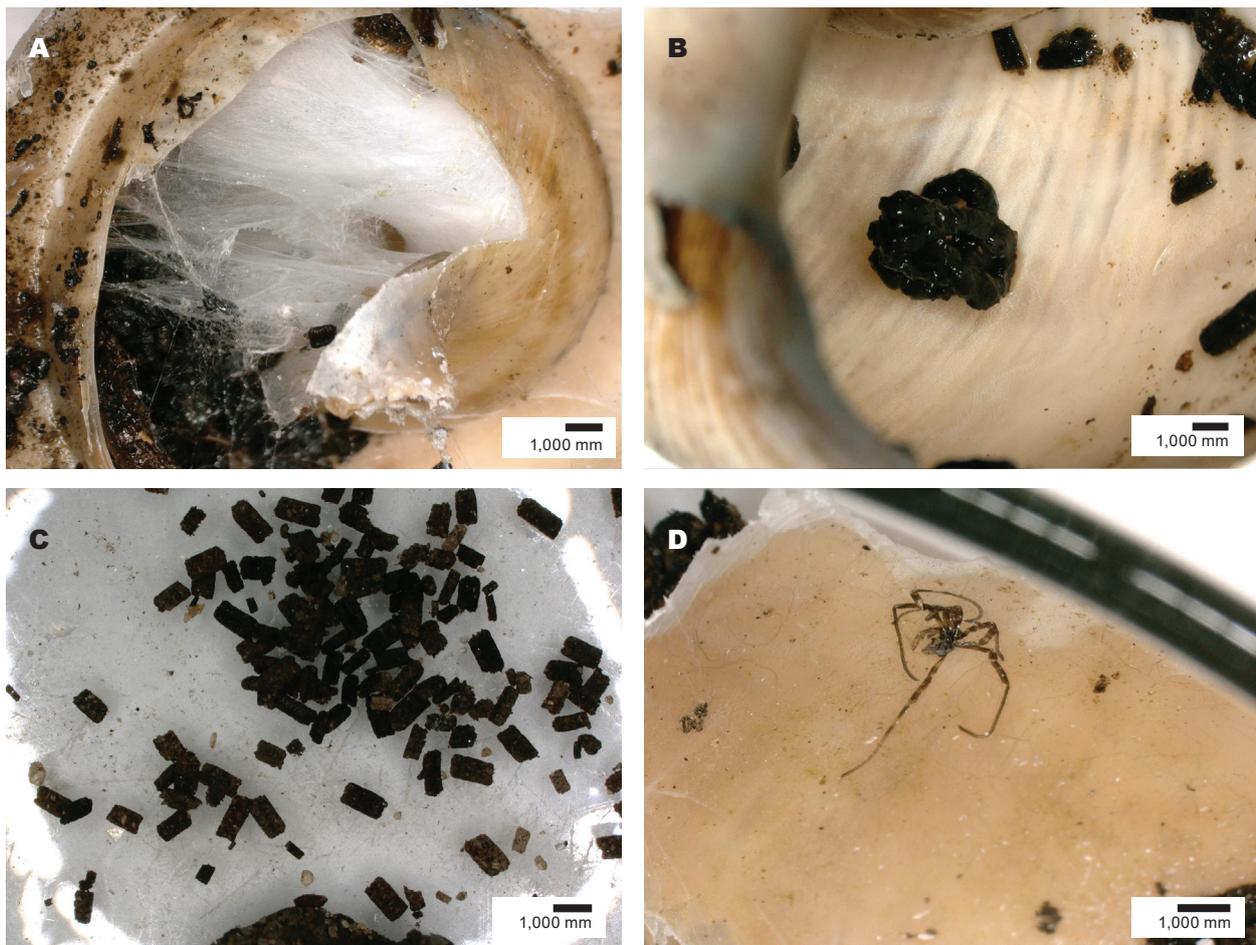


Figure 3. Indirect signs of shell utilization with (A) Araneae silk remains, (B) Gastropoda faeces, (C) Isopoda faeces and (D) Araneae exuvia.

4.1 Number of shell adopters and taxonomic groups

Bogusch et al. (2019) on average reared 4.4 to 5.2 insects per 100 shells collecting all large and medium-sized shells of different snail species in Czech Republic, including *H. pomatia*. *Helix pomatia* shells in our study area on average had 2.2 terrestrial invertebrate individuals per shell (averages of 1.7 in autumn and 2.5 in summer), which may suggest that shells of this species are particularly important for shell adopters. However, in contrast to Bogusch et al. (2019), utilization is not defined as reproduction in this study, but also includes the use of shells for shelter from unfavourable microclimatic conditions or predators, foraging or other activities. Previous studies highlighted the significant influence of season on the utilisation of shells (Moreno-Rueda et al. 2008, Romero et al. 2020), which was confirmed in this study. The higher average abundance of shell adopters in shells collected in summer compared

to shells collected in autumn suggests that *H. pomatia* shells play a particularly important role as shelter from temperature extremes during summer months. The number of individuals per shell was on average higher in shells placed in herbaceous vegetation compared to locations under trees. Herbaceous vegetation, such as *Urtica dioica* and *Aegopodium podagraria* decay in winter and cover the shells in these months. The resulting microclimate can be several degrees cooler in summer compared to the air temperature (Keppel et al. 2017) and in winter often remains above the freezing point (Perry 2013). Norton et al. (2014) showed that temperatures below leaf litter in summer are lower than below grass cover. However, shells were placed on top of the leaf litter in February in this study and those potential microclimatic benefits do not apply in our study. It is therefore more likely that soil invertebrate activity was generally higher in study plots dominated by herbaceous vegetation and that the average number of shell adopters reflects these differences.

4.2 Composition of shell adopters

The high occurrence of gastropods observed in *H. pomatia* shells independent of sampling period, indicates that these species frequently seek shelter from cold and hot temperatures in other gastropod shells. In contrast to snails, slugs were rarely observed as shell adopters (1% in autumn and 7% in summer). Larger species of slugs may not be capable of moving into snail shells, as the biggest slug found in a shell [*Limax maximus* (Linnaeus, 1758)] was about 5cm long. The most frequently observed slug species (*A. intermedius*), as well as another snail species (*D. rotundatus*), showed a preference for the widest *H. pomatia* shells in our study.

Slugs generally seem to prefer alternative shelter habitats over empty snail shells (Moreno-Rueda 2007).

In total, 18% of all individuals found in shells were Acari, of which Oribatid mites were most abundant (61% of all Acari). Mite communities includes species with development periods of up to 5 years and adults may survive up to 3 years (Søvik et al. 2003, Søvik & Leinaas 2003). Hansen (1999) previously suggested that in Oribatid mites, eggs and soft-bodied juveniles are more vulnerable to predation than adults. Snail shells therefore offer a particularly valuable shelter habitat for earlier development stages. Due to deposition of faeces by other shell adopters, fungi colonise and develop in shells (Fig. 4 A–C). Several fungivorous oribatid species, and

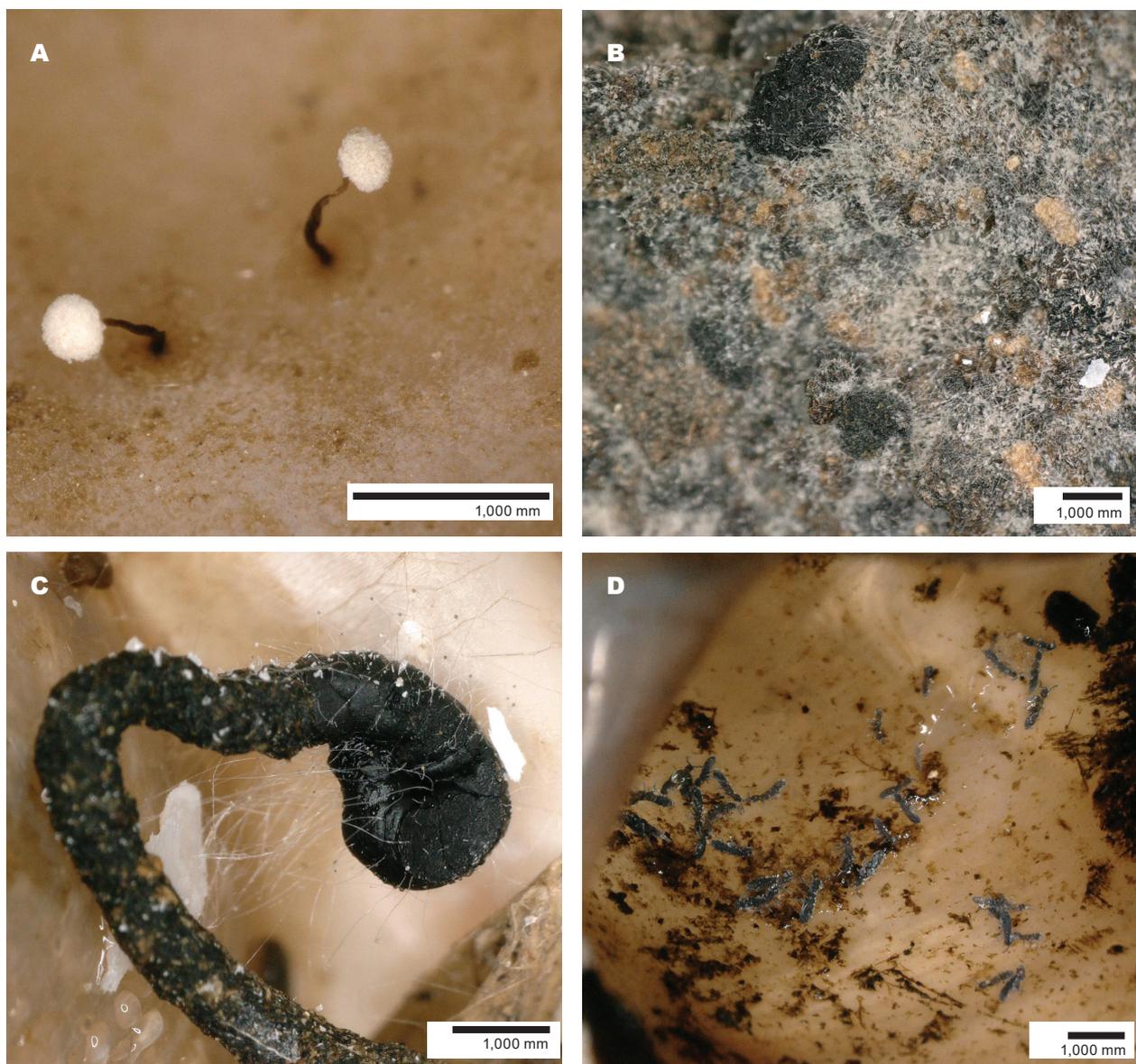


Figure 4. Indirect signs of shell utilization with (A–C) fruiting bodies and hyphal networks growing inside shells mainly on Gastropoda faeces and (D) large group of 95 Entomobryomorpha Collembola in a single shell.

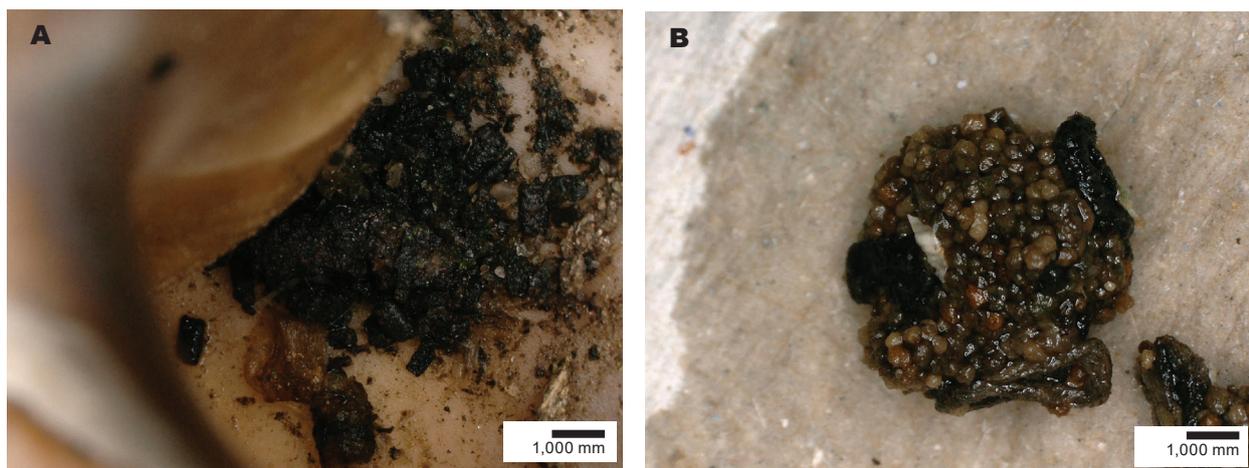


Figure 5. Indirect signs of shell utilization with faeces of (A) Isopoda and (B) Dermaptera deposited on top of Gastropoda faeces.

also Collembola may therefore colonise shells for shelter and feeding (Hanlon 1981, Dromph 2001). A particularly impressive example in our study was a single *H. pomatia* shell that was colonised by 95 Entomobryomorpha Collembola (Fig. 4D).

Empty snail shells, utilized as a nesting resource, are a key factor in conserving endangered bee species (Bogusch et al. 2020). Our results further highlight their benefits for a large range of soil invertebrate taxa. The importance of snail shells as shelter for isopods, regarding moulting, avoidance of water loss and provision of food resources was previously documented (Dias et al. 2012, Rupp & Ziegler 2019, Leclercq-Dransart et al. 2019). Snail shells reduce mortality, but different isopod species have specific preferences (Hassall & Tuck 2007, Hassall et al. 2018). Broly et al. (2013) highlighted that isopods prefer shelter habitats, in which faeces are present. Shells of *H. pomatia* seem to be an ideal shelter for isopods, due to the quantity of faeces observed in our study and the relatively large size of shells. Gastropod faeces inside shells were often covered by faeces of Isopoda and Dermaptera (Fig. 5A&B), suggesting frequent secondary colonisation. These observations indicate shell colonisation by Isopoda and Dermaptera that is facilitated by pioneer gastropod colonizers.

5. Conclusions

Shells of the Roman snail provide important multipurpose benefits for soil meso- and macrofauna that goes beyond the previously reported advantages for bees or isopods. A wide range of invertebrates such as Collembola, Acari, Dermaptera and spiders frequently colonised *H. pomatia* shells. Numbers were particularly

high in habitats that were dominated by herbaceous vegetation and in summer indicating that the addition of shells of *H. pomatia* from heliculture offers potential for the conservation of soil invertebrates in local restoration programs. It is notable, that only 44% of all shells could be re-collected in this study and future studies should address the reasons for shell losses from local habitats. The study area is close to urban centres and frequently visited by humans as recreational area. Together with losses to potential predators (e.g. birds) or relocation of shells by shell adopters, a certain number of shells were probably lost due to removal by humans.

6. Acknowledgement

We acknowledge the comments by the editor and two anonymous referees that helped improving the manuscript. We are grateful to Heike Reise and Johanna Simchen from the Senckenberg Museum of Natural History Görlitz for help with the determination of gastropods. We also would like to thank Benjamin Schnerch who helped with the determination of the spiders and Liz Lethal for Heteroptera identification.

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Supplementary Tables 1–3

Table S1. Dominant vegetation, latitude and longitude at each study plot in each subpopulation.

Subpopulation & study plot	Dominant vegetation	Latitude	Longitude
1-1	<i>Rubus</i> sp.	N 51°44'41.28	E 14°16'59.58
1-2	<i>Urtica dioica</i>	N 51°44'40.85	E 14°16'59.55
1-3	Trees	N 51°44.41.81	E 14°16'57.94
2-1	Trees	N 51°44'38.91	E 14°17'06.07
2-2	<i>Aegopodium podagraria</i>	N 51°44'37.55	E 14°17'10.62
3-1	Trees	N 51°44'37.00	E 14°17'54.08
3-2	<i>Urtica dioica</i>	N 51°44'37.18	E 14°17'53.26
4-1	Trees	N 51°44'38.50	E 14°17'47.55
5-1	<i>Aegopodium podagraria</i>	N 51°44'47.46	E 14°18'08.31
5-2	Trees	N 51°44'48.45	E 14°18'09.29
5-3	<i>Rubus</i> sp.	N 51°44'48.33	E 14°18'08.48
6-1	<i>Urtica dioica</i>	N 51°44'47.59	E 14°17'59.82
6-2	<i>Aegopodium podagraria</i>	N 51°44'46.86	E 14°17'59.64
7-1	<i>Aegopodium podagraria</i>	N 51°44'28.33	E 14°18'38.75
7-2	<i>Rubus</i> sp.	N 51°44'28.43	E 14°18'32.93
8-1	Trees	N 51°44'47.23	E 14°18'05.13

Table S2. List of shell adopters collected in autumn and summer and in study plots dominated by herbaceous vegetation or trees at the level of taxonomic resolution considered in this study and the number of shells observed during the study with shell adopters from each taxon.

Higher taxon	Lower taxon	Autumn	Summer	Herbs	Trees	Shells
Acari	Astigmatina	4	32	29	7	28
Acari	Mesostigmata	26	13	27	12	29
Acari	Oribatida	61	100	132	29	97
Acari	Trombidiformes	8	10	15	3	17
Araneae	Clubionidae	0	1	1	0	1
Araneae	Gnaphosidae	4	1	1	4	5
Araneae	Linyphiidae	17	15	21	11	29
Araneae	Liocranidae	1	0	1	0	1
Araneae	Lycosidae	1	0	0	1	1
Araneae	Salticidae	3	0	0	3	3
Chilopoda	Lithobiidae	1	0	1	0	1
Coleoptera	Aderidae	1	1	2	0	2
Coleoptera	Curculionidae	2	4	1	5	6
Coleoptera	Ptiliidae	1	0	0	1	1
Coleoptera	Pyrochroidae	2	0	1	1	2
Coleoptera	Staphylinidae	1	1	1	1	2
Collembola	Entomobryomorpha	56	249	279	26	97
Collembola	<i>Orchesella cincta</i>	1	4	0	5	5
Collembola	<i>Orchesella vilosa</i>	3	8	7	4	11
Collembola	Poduromorpha	33	31	46	18	48
Collembola	Symphyleona	45	2	23	24	39
Collembola	<i>Tomocerus longicornis</i>	0	1	1	0	1
Collembola	<i>Tomocerus minor</i>	0	3	0	3	3
Dermaptera	<i>Forficula auricularia</i>	2	69	2	69	14

Continued Table S2.

Higher taxon	Lower taxon	Autumn	Summer	Herbs	Trees	Shells
Diplopoda	Blaniulidae	1	1	1	1	2
Diplopoda	Julidae	1	6	6	1	7
Diplopoda	Polydesmidae	3	10	6	7	12
Diplopoda	Polyxenidae	0	1	1	0	1
Hymenoptera	Formicidae	5	16	8	13	17
Gastropoda	<i>Aegopinella</i> sp.	1	0	0	1	1
Gastropoda	<i>Alinda biplicata</i>	0	1	1	0	1
Gastropoda	<i>Arianta arbustorum</i>	1	0	1	0	1
Gastropoda	<i>Arion circumscriptus</i>	0	1	0	1	1
Gastropoda	<i>Arion distinctus</i>	1	0	0	1	1
Gastropoda	<i>Arion intermedius</i>	0	1	0	1	1
Gastropoda	<i>Arion vulgaris</i>	0	1	0	1	1
Gastropoda	<i>Cepaea nemoralis</i>	7	2	5	4	8
Gastropoda	<i>Cepaea</i> sp.	20	34	20	34	52
Gastropoda	Clausiliidae	0	1	1	0	1
Gastropoda	<i>Cochlicopa lubrica</i>	4	5	2	7	8
Gastropoda	<i>Discus rotundatus</i>	17	11	26	2	24
Gastropoda	<i>Lucilla scintilla</i>	1	0	0	1	1
Gastropoda	Helicidae	1	0	1	0	1
Gastropoda	<i>Helix pomatia</i>	3	0	1	2	3
Gastropoda	<i>Limax maximus</i>	0	2	1	1	2
Gastropoda	<i>Oxychilus draparnaudi</i>	1	0	0	1	1
Gastropoda	<i>Punctum pygmaeum</i>	3	5	4	4	7
Gastropoda	<i>Trochulus hispidus</i>	11	4	15	0	14
Gastropoda	<i>Trochulus</i> sp.	2	0	2	0	2
Gastropoda	<i>Truncatellina cylindrica</i>	1	3	1	3	4
Gastropoda	<i>Truncatellina</i> sp.	1	2	0	3	3
Gastropoda	<i>Vallonia costata</i>	4	0	3	1	4
Gastropoda	<i>Vallonia</i> sp.	1	2	2	1	3
Gastropoda	<i>Vertigo substriata</i>	0	1	1	0	1
Gastropoda	Vitrinidae	0	1	0	1	1
Gastropoda	<i>Vitrina pellucida</i>	3	0	1	2	3
Gastropoda	Zonitidae	1	0	0	1	1
Heteroptera	<i>Kleidocerys resedae</i>	0	1	1	0	1
Heteroptera	Rhyparochromidae larvae	4	1	3	2	4
Heteroptera	<i>Scolopostethus affinis</i>	2	2	3	1	4
Heteroptera	<i>Scolopostethus thomsoni</i>	5	0	3	2	5
Isopoda	<i>Armadillidium vulgare</i>	11	73	48	36	59
Isopoda	<i>Hyloniscus riparius</i>	3	1	3	1	4
Isopoda	<i>Philoscia muscorum</i>	7	21	15	13	25
Isopoda	<i>Platyarthus hoffmannseggii</i>	1	1	2	0	2
Isopoda	<i>Porcellio scaber</i>	16	43	28	31	40
Isopoda	<i>Porcellio</i> sp.	0	1	0	1	1
Isopoda	<i>Porcellio spinicornis</i>	9	1	6	4	8
Isopoda	<i>Trachelipus rathkii</i>	44	47	64	27	64
Orthoptera	<i>Tetrix subulata</i>	1	0	1	0	1
Pseudoscorpiones	<i>Neobisium</i> sp.	3	11	13	1	10

Table S3. The number of shells with signs of utilization collected in autumn and summer and in study plots dominated by herbaceous vegetation or trees.

	Autumn	Summer	Herbs	Trees
Unidentified eggs	0	2	1	1
Gastropoda faeces	19	94	60	53
Formicidae nest	3	13	12	4
Isopoda faeces	97	149	127	119
Araneae egg sacs	10	1	4	7
Araneae silk remains	29	30	24	35
Araneae exuvia	14	10	12	12
Dermaptera exuvia	1	3	1	3