

# **Population ecology of the Roman snail (*Helix pomatia* L. 1758) in Cottbus, Brandenburg**

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By

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I hereby confirm that my thesis entitled “Population ecology of the Roman snail (*H. pomatia*) in Cottbus, Brandenburg” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

Cottbus

Claudia Tluste

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The following publications were included within this thesis:

*Tluste, C., Bröring, U., Němec, T. and Birkhofer, K. (2020) “Morphometric traits of shells determine external attack and internal utilization marks in the Roman snail in eastern Germany.”, Web Ecology 20, pp. 1–8, DOI: 10.5194/we-20-1-2020*

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## Summary

The high extinction rate among species worldwide, and especially among molluscs is well known and it is expected that by the year 2539 almost 75% of all freshwater mollusc species within Europe will be lost. The situation for terrestrial molluscs may be the same, with the main extinction threats being transformation of natural ecosystem by construction of residential and commercial infrastructure and the extension of agriculture. The Roman snail (*Helix pomatia* L. 1758) has been part of human culture for centuries and is therefore well known among society in Germany and Europe. Protected by law as an endangered species in several regions, utilized for human consumption and at the same time regarded and treated as a pest the conservation of this species is difficult.

The overall research aim was to create a deeper understanding of *H. pomatia* and its functional role in the studied ecosystem to highlight the importance of the conservation of this charismatic species. The study area for *H. pomatia* populations is a landscape protection area in the Southwest of Cottbus, called “Sachsendorfer Wiesen”, which was restricted from agricultural use in 1990. Since then, different habitats developed with a steadily growing diversity of fauna and flora. Eight subpopulations of *H. pomatia* were identified in that area to study its role within the ecosystem from the perspective of the food web (research chapter 1), its contribution of empty shells as a microhabitat to soil organisms (resulting from predation or other sources of mortality) (research chapter 2) and its influence on vegetation by showing food preferences (research chapter 3). The latter, due to the fact, that a strong predation pressure can lead to a limited choice of habitats for this species, which again leads to higher pressure on the local vegetation and a limited possibility of shells being used as a microhabitat.

The first research chapter addresses the relationships between *H. pomatia* individuals and subpopulations and their predators. Snail shells were analysed for the total number and percentage of shells that showed external attack marks by predators (207 out of 642 - 32%) and internal utilization marks by Diptera pupae (159 out of 353 – 45%). Those percentages were correlated to morphometric traits of shells to identify which subpopulations are under highest predation pressure. A sizeable proportion of the shells in local subpopulations indicated signs of external attack and internal utilization, and both utilization types were positively correlated ( $R = 0.79$ ;  $P = 0.020$ ). External attacks by predators were more regular in larger shells and internal utilization by Diptera was more frequent in shells with higher body density. These findings indicate a substantial pressure by predators and potential facultative parasitoids on *H. pomatia* populations in the study area.

The second research chapter focuses on the shells of *Helix pomatia* and their value as microhabitat for shell adopters in different dominant vegetation forms and during two sample periods. In total, 91.4 % of all collected shells (618 in total) were inhabited by shell adopters and the average number of shell adopters was 1.5 time higher in shells, that were collected in summer, than among shells, that were collected in autumn. The number of shell adopters per shell was 1.5 times higher in study areas dominated by herbaceous vegetation, than in study areas dominated by trees. Shell width ( $F_{1,11} = 2.79$ ,  $P = 0.008$ ), but not shell height ( $F_{1,11} = 1.82$ ,  $P = 0.078$ ) affected the composition of shell adopter communities significantly. Shells with a larger width were more repeatedly colonized by another gastropod species, as *Discus rotundatus* (O. F. Müller, 1774) than less wide shells. Shells of *Helix pomatia* offer crucial benefits for a wide range of soil organisms, particularly in habitats that were dominated by herbaceous vegetation. This result highlights the value of *H. pomatia* for the conservation of a broad range of species and indicates that indirect benefits of the species presence in local habitats are important for biodiversity conservation overall.

The third research chapter focuses on food preferences of *H. pomatia*. The results show that *H. pomatia* has a pronounced preference for *Urtica dioica* (35% of all 697 feeding interactions) and plant litter (44%) as food resources, while generally only feeding on 27 out of 143 available plant species in the study area. The general importance of *U. dioica* as food plant for terrestrial snail species in general is confirmed by a literature review of 17 additional studies for 19 other terrestrial snail species. The width and height of the snail shells in *H. pomatia* was related to the feeding height of individuals in the vegetation. Smaller, juvenile snails consumed plant material significantly higher in vegetation ( $384\text{mm} \pm 327\text{mm}$  standard deviation) compared to adult individuals ( $68\text{mm} \pm 194\text{mm}$ ) ( $F_1, 695=252.49$ ;  $P<0.001$ ). This study highlights the potential of the plant species *U. dioica* as resource to attract potential pest species away from crops and emphasizes the need to further study diets of terrestrial snail species to improve conservation strategies.

These results highlight the importance of *H. pomatia* in the studied ecosystem Sachsendorfer Wiesen. Individuals of *H. pomatia* are an important food source for predators and host for parasitoids, the shells offer habitat and refuge for soil organisms and as a relatively specialized herbivore and decomposer *H. pomatia* contributes to herbivory and nutrient cycling in ecosystems. Conservation efforts depend on the cooperation with land-owners, land-users and informed strategies to conserve and restore habitats to the benefit of this species. Highlighting the importance of the species for other organisms in this study hopefully motivates future conservation efforts.

## Zusammenfassung

Ein großes Artensterben bedroht viele Spezies weltweit, insbesondere auch die Mollusken. Im Jahr 2539 werden voraussichtlich 75% aller Frischwassermollusken in Europa ausgestorben sein. Die Situation ist für Landmollusken ähnlich, da auch innerhalb dieser Gruppe Veränderungen von Ökosystemen durch den Bau von Wohn- und Geschäftsgebäuden und die Ausweitung der Landwirtschaft voranschreiten. Die Weinbergschnecke (*Helix pomatia* L. 1758) ist seit vielen Jahrhunderten ein Teil der menschlichen Kultur und generell der Bevölkerung in Deutschland und Europa gut bekannt. In vielen Regionen ist sie gesetzlich als bedrohte Art geschützt, wird aber auch zum menschlichen Verzehr gesammelt und von Gärtnern als Schädling bewertet was den Erhalt der Art erschwert.

Das Ziel dieser Untersuchungen ist es ein besseres Verständnis zu bekommen, von der Rolle der Weinbergschnecke im untersuchten Ökosystem und daraus Notwendigkeiten und Maßnahmen zum Schutz der Art abzuleiten. Das Untersuchungsgebiet, das Landschaftsschutzgebiet Sachsendorfer Wiesen, liegt im Südwesten von Cottbus und wurde 1990 aus der landwirtschaftlichen Nutzung ausgeschlossen. Seitdem konnten sich verschiedene Habitate entwickeln, welche eine Zunahme der Diversität der Flora und Fauna bedingen.

In diesem Gebiet wurden acht Teilpopulationen von *H. pomatia* identifiziert, um dessen Rolle innerhalb des Ökosystems zu untersuchen. Zum einem aus der Perspektive des Nahrungsnetzes (Forschungskapitel 1), anschließend, den Beitrag leerer Gehäuse, die durch Prädation oder andere Mortalitätsquellen entstehen, als Lebensraum für Bodenorganismen (Forschungskapitel 2) und letztendlich die Ernährungsökologie von *H. pomatia* (Forschungskapitel 3). Letzteres unter anderem weil ein starker Druck durch Prädation zu einer geringeren Auswahl an Habitaten für diese Art führen kann, was wiederum zu einem erhöhten Fraßdruck auf die besiedelte Vegetation und einer örtlich begrenzten Verfügung von leeren Schneckenschalen führt.

Das erste Forschungskapitel der vorliegenden Arbeit befasst sich mit der Beziehung zwischen *H. pomatia*, Fressfeinden und Parasitoiden. Schneckengehäuse wurden dazu auf äußere Zeichen von Angriffen durch Fressfeinde, bzw. auf interne Spuren der Nutzung durch Dipteren untersucht. Diese Zeichen wurden ins Verhältnis gesetzt zur Größe der Gehäuse. In den untersuchten Subpopulationen zeigte ein großer Teil der Gehäuse Zeichen von äußeren Angriffen (207 von 642 - 32%) und innerer Nutzung durch Parasitoide (159 von 353 – 45%). Diese Prozentteile wurden dann im Bezug auf die körperlichen Merkmale der Schalen hin untersucht, um dessen Einfluss auf den Prädationsdruck festzustellen. Ein großer Anteil der



Schalen in den einzelnen Unterpopulationen zeigte Zeichen von äußeren Angriffen und innerer Nutzung und beide Arten korrelierten positiv miteinander ( $R = 0.79$ ;  $P = 0.020$ ). Der Anteil der Gehäuse mit äußeren Angriffsspuren war höher in Subpopulationen mit größeren Gehäusen, während die innere Nutzung durch Fliegen in Subpopulationen am häufigsten war, welche eine hohe Körperdichte aufwiesen. Die Resultate zeigen einen hohen Druck durch Fressfeinde und mögliche Parasitoide auf die Population von *Helix pomatia* im Untersuchungsgebiet.

Das zweite Forschungskapitel konzentriert sich auf die Gehäuse von *H. pomatia* und deren Nutzung als Mikrohabitat für Bodenorganismen. Hierzu wurde die Besiedlung leerer Gehäuse in unterschiedlichen Vegetationsformen und in zwei Sammelperioden untersucht. Insgesamt wurden 91,4% (von insgesamt 618) aller eingesammelten Gehäuse von anderen Tierarten genutzt, wobei die Anzahl der gefundenen Individuen im Sommer 1,5-mal höher war als im Herbst. Die Anzahl an Nutzern war ebenfalls 1,5-mal höher in Gebieten mit einer gut ausgebildeten Krautschicht im Vergleich zu Gebieten mit Bäumen ohne Krautschicht. Die Breite der Gehäuse ( $F_{1,11} = 2.79$ ,  $P = 0.008$ ) aber nicht deren Höhe ( $F_{1,11} = 1.82$ ,  $P = 0.078$ ) beeinflusste die taxonomische Zusammensetzung der Nutzer. Gehäuse mit einer größeren Weite wurden besonders oft von *Discus rotundatus* (O. F. Müller, 1774) genutzt. Insgesamt stellen die Gehäuse der Weinbergschnecke wichtige, multifunktionale Habitate für eine hohe Anzahl an Bodenorganismen dar, vor allem im Sommer und in Habitaten mit ausgeprägter Krautschicht. Diese Resultate bekräftigen die Wichtigkeit von *H. pomatia* hinsichtlich des Schutzes einer Vielzahl anderer Arten und die indirekten Vorteile durch die Anwesenheit dieser Art für den Erhalt der Biodiversität im Allgemeinen.

Im dritten Forschungskapitel wurde die Ernährungsökologie von *H. pomatia* untersucht. Die Ergebnisse zeigen, dass *H. pomatia* eine Präferenz für *Urtica dioica* als wichtigste Nahrungspflanze zeigt (35% von 697 Fressaufnahmen) und insbesondere auch Laubstreu (44%) als Nahrung bedeutsam ist. Von 143 lokal in den Subpopulationen verfügbaren Pflanzen wurden nur 27 Arten gefressen. Die Bedeutung von *U. dioica* als Nahrungspflanze wurde im Rahmen einer Literaturrecherche auch in 17 weiteren Studien bestätigt, welche 19 weitere Landschneckenarten beinhaltet. Die Breite und Höhe der Gehäuse stehen im Zusammenhang zur Höhe der fressenden Schnecken in der Vegetation. Kleinere, juvenile Schnecken konsumierten Nahrung höher ( $384\text{mm} \pm 327\text{mm}$  Standardabweichung) in der Vegetation als erwachsene Schnecken ( $68\text{mm} \pm 194\text{mm}$ ) ( $F_1, 695 = 252.49$ ;  $P < 0.001$ ). Diese Studie unterstreicht das Potenzial der Pflanzenart *U. dioica* als Ressource, um potenzielle Schädlingsarten von Nutzpflanzen wegzulocken, und unterstreicht die Notwendigkeit, die

Ernährungsgewohnheiten von Landschneckenarten weiter zu untersuchen, um Artenschutzstrategien zu verbessern

Zusammenfassend unterstreichen diese Ergebnisse die Bedeutung von *H. pomatia* in dem untersuchten Ökosystem Sachsendorfer Wiesen. Individuen von *H. pomatia* sind eine wichtige Nahrungsquelle für Raubtiere und Wirte für Parasitoide, die Schalen bieten Lebensraum und Zuflucht für Bodenorganismen, und als relativ spezialisierter Pflanzenfresser und Zersetzer trägt *H. pomatia* zur Herbivorie und zum Nährstoffkreislauf in Ökosystemen bei. Die Artenschutzbemühungen hängen von der Zusammenarbeit mit Landbesitzern und Landnutzern sowie von sachkundigen Strategien zur Erhaltung und Wiederherstellung von Lebensräumen zum Nutzen dieser Art ab. Die Hervorhebung der Bedeutung der Art für andere Organismen in dieser Studie motiviert hoffentlich künftige Schutzbemühungen.

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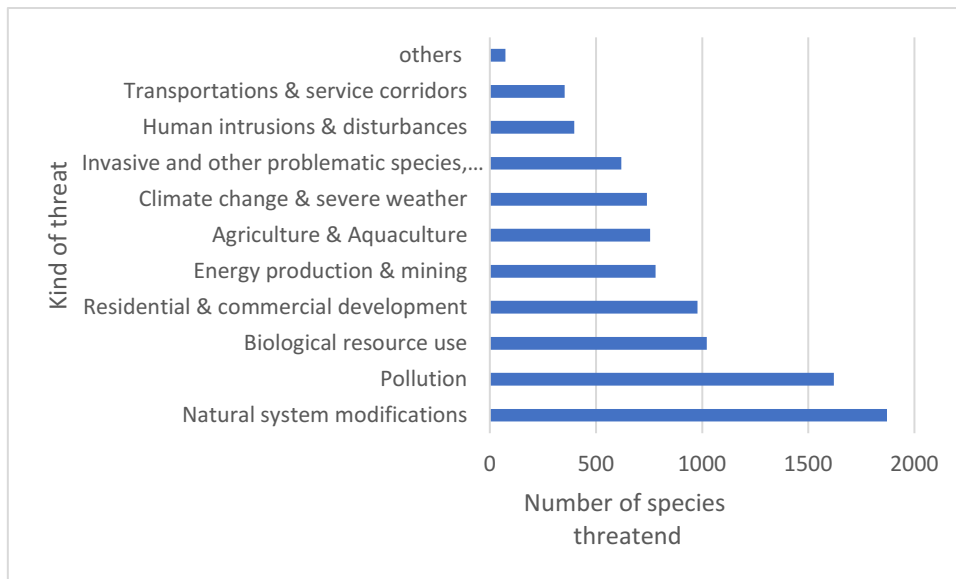
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## I. General introduction

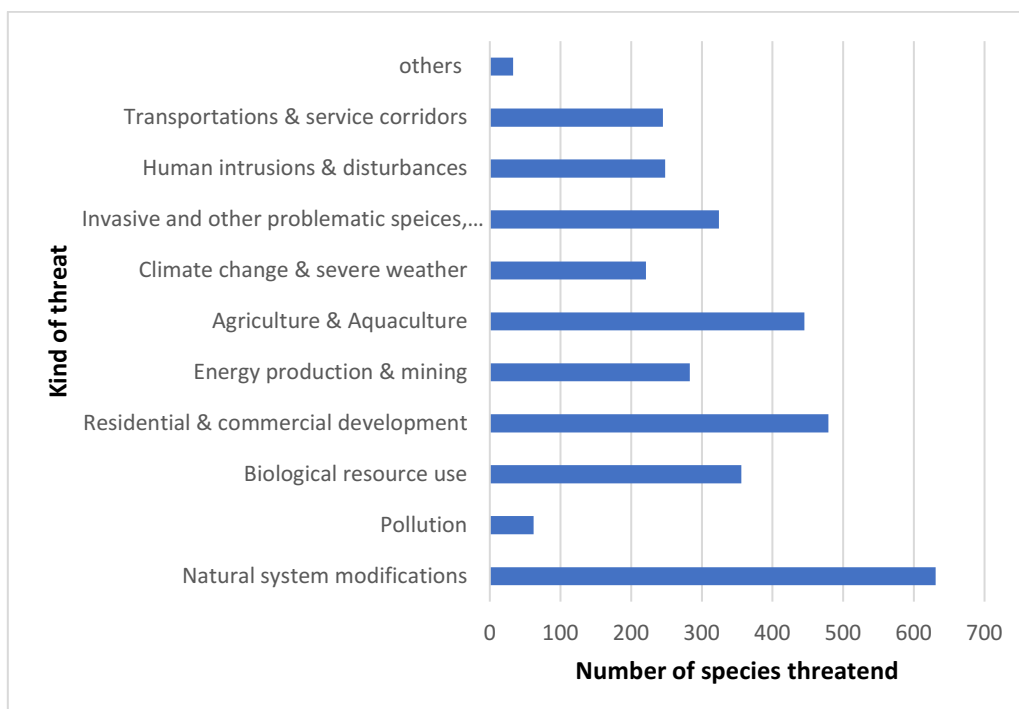
### 1.1 Conservation status of terrestrial gastropods

Earth experiences a very high extinction rate of species worldwide, which is 100 times higher among mammals and vertebrates than ever before, expecting a second wave in 2100 (Ceballos et al., 2015; Andermann et al., 2020). Andermann et al. (2020) showed that the extinction rate of mammal species since the Late Pleistocene can be predicted with an accuracy of 96 to 97% by the growth of the human population and the resulting changes in land use, which lead to a fragmentation of habitats. If mammal extinction is stopped right now, it would take 4-5 million years for mammal biodiversity to return to its pre-Pleistocene level (Davis et al., 2018). The situation is even worse for freshwater molluscs, as one third of all freshwater molluscs worldwide is threatened by extinction (Böhm et al., 2020). Within the last 1500 years 7.5-13% of all molluscan species have already gone extinct (Cowie et al., 2017). During the Cretaceous–Paleogene mass extinction, 92.5% of all freshwater molluscs got extinct, taking 6.9 million years to recover. The current extinction dynamic is three times faster than this previously observed extinction wave and by 2539 75% of all freshwater molluscs within Europe can be lost (Neubauer et al., 2021). The reason for this rapid and severe loss among gastropods partly stems from often small geographic range and poor colonisation abilities of many species (Thompson et al. 2017, Neubauer and Georgopoulou, 2021). Bros et al. (2016) showed that climate, habitat, and elevation have significant influence on the distribution pattern of gastropod species, but that factors at the microhabitat level are more important including edaphic conditions and the chemical and taxonomic composition of plant communities in the microhabitat. Range-restricted species are more severely affected by land clearing and predation by invasive species (Chiba, 2011). Molluscicides are an additional local threat to gastropods, but most probably have a limited influence on the overall extinction rate of molluscs worldwide. As Wang et al. (2020) highlight, molluscicides have a stronger negative impact on non-gastropod species, soils and humans that come in contact with these agrochemicals. Figure 1 gives an overview about the most actual threats towards molluscs worldwide according to the International Union for Conservation of Nature (IUCN) Red lists.



*Figure 1 Threats to molluscs, IUCN Red List, 2022*

A relative difference can be seen in the ranking of threats between molluscs in general and threat for terrestrial snails (Figure 2). Both are severely threatened by the modification of natural systems, but terrestrial snails suffer less from pollution than other molluscs. Land snails are more severely threatened by the construction of residential and commercial developments as well as the extension of agriculture, (IUCN, 2022).



*Figure 2 Threats terrestrial snails, IUCN Red Lists, 2022*

Strong et al. (2008) highlight that the status of the great majority of taxa among freshwater molluscs is unknown, a situation that is exacerbated by a lack of experts and critical baseline data relating to the distribution, abundance, life history, physiology, morphology, and diet of species. Thus, the already considerable, magnitude of extinction and high levels of threat indicated by the IUCN Red List of Threatened Species is most likely underestimating the problem (see also Régnier et al. 2009).

## 1.2 Ecology of terrestrial snails

Parkyn and Newell (2013) highlighted in their review on the ecology of terrestrial land snails in Australia the scarcity of available information. Species are described as well as their distribution, but just limited knowledge is available on habitat preferences and conservation possibilities. Dahirel et al. (2014, 2015 b, 2017) conducted different studies to understand the dispersal willingness and ability of different species. Dispersal is an important ecological factor, as it ensures the spread of species, the flow of genes and the reduction of competition (Dahirel et al., 2014). It was confirmed that the humidity level as well as the rainfall were the main weather variables, that affected emigration and transience (Dahirel et al., 2014). However, species that are highly specialised on their habitat, show a lower dispersal tendency, have a smaller foot and are slower than general species (Dahirel et al., 2015 b), which leads to a higher vulnerability regarding habitat fragmentation and destruction. In 2017 Dahirel et al. could even show, that especially sub-adults of *Cornu aspersum* and bolder individuals were more dispersive than older and less bold individuals. This highlights the narrowed possibilities of many molluscan species to explore new habitat. Horsák et al. (2009) shows that the response of local snail assemblages along a gradient of habitat degradation can be generalised as a gradual decline in species richness, especially of rare and anthropophobic species. Which only emphasises the need for a natural habitat. Studies confirm different variables, that influence the dispersion of snails: tree cover, habitat diversity, productivity of ground vegetation, and location on an esker ridge (Astor et al., 2014). Especially the proportion between the coverage of litter and herbaceous vegetation cover, as well as the diversity of litter are important (Szybiak et al., 2009).

There is a strong dependency between snails and litter. Snails do feet on litter and contribute to a good litter decomposition, though the contribution varies between 0,35% till 1,5% of the annual litter production (Mason, 1970a + b; Jennings and Barkham 1976). Theenhaus and Scheu (1996) could show that the cycling of Carbon, Nitrogen and Phosphorus is accelerated

by slug activity. Especially bigger snails, have a higher consumption rate and control a greater proportion of available resources (Hausdorf, 2007; Astor et al., 2015). Even many snails prefer a humid or wet surrounding, there are several species like *Ceriuella virgata* (Da Costa), that adapted to a dry and hot climate (Schweitzer et al., 2019). Terrestrial snails also play an important part in the food web, were many of them are used as a source of calcium (Allen, 2004; Barker & Efford, 2004; Gosler, 2006), but more study needs to be done to get a detailed picture. Most of the studies that were conducted regarding the ecology of terrestrial snails highlight small individual findings as the infection by mites (Wacker, 2008) or the increase of yeast biodiversity due to snails (Akan et al, 2020) but an overall picture, comparable with our knowledge on the ecology of mammals still needs to be established.

### 1.3 *Helix pomatia* as a case species for terrestrial snails

The species *Helix pomatia* L. 1758 (Figure 3) is the most well-known snail in Germany and throughout Europe. The Nature Protection Society of Germany (NABU) used this fact and the large size of the species in a citizen science project asking the public to share the location of *H. pomatia* observations to create distribution maps (NABU Brandenburg, 2023). In Hungary, such research received feedback from 123 participants within the first five days, highlighting the awareness of the people regarding this species (Páll-Gergely et al., 2019). The currently known latitudinal distribution range of *H. pomatia* spans from Greece to Scandinavia, and its longitudinal range extents from westernmost Russia to England (Neubert, 2014).



*Figure 3 Helix pomatia individual, by Christian Ketzmerick*



*Helix pomatia* is well known as human food that has been part of human history since the Roman Empire and throughout the Middle Age (Bonnemain, B., 2005), hence the common name Roman snail. Due to a high demand of snails, exploitation of natural populations takes place in many countries, leading to a decline and the extinction of local populations (Andreev, 2006; Błoszyk et al, 2010; Gheoca, 2013). This resulted in a specific protection status in some European countries. Table 1 gives an overview about different Red Lists that consider *H. pomatia* in Europe. As only Great Britain, Netherland and Poland consider this species as scarce or at risk, it is clear, that *H. pomatia* still has stable populations in most countries. However, as Andreev and Gheoca were highlighting, this can change in the future and the fact that this species is perceived as a pest in vegetable and ornamental crops in Western Europe (Port & Ester, 2002) adds another threat to local populations.

*Table 1 Overview of selected Red Lists within Europe regarding Helix pomatia*

<b>Red list</b>	<b>Red list status</b>	<b>Source</b>
IUCN Red List	Least concern – population stable	IUCN Red List 2021
European Red List of non-marine molluscs	Least concern – population stable	Cuttelod et al., 2011
Red List Germany	Safe – population stable	Rote Liste Zentrum, 2021
Red List Great Britain	Nationally scarce	Seddon et al., 2014
Red List Netherland	At Risk – population declining	Bruyne et al., 2003
Red List Austria	Least concern – population declining	Reischütz and Reischütz, 2007
Red List France	Least concern	INPN, 2023
Red List Republic of Moldova	Least concern	Coadă et al., 2017
Red List Poland	Near threatened	Polska Czerwona Księga Zwierząt, 2009
Red List Slovenia	Least Concern	Uradni list, 2002
Red List Switzerland	Least concern – population stable	Rüetschki et al., 2012

*Helix pomatia* prefers calcareous soils in forests, at hillsides, in vineyards or gardens and parks. The species prefers habitats with groves and tall forbs (Wiese, 2016) and highly depends on a habitat that persists over time (Gheoca et al., 2021). A study in Poland suggests that the species occurs most abundantly in anthropogenic habitats situated in areas of high landscape patchiness (Dyduch-Falniowska et al., 2001). Previous conservation projects tried to establish new colonies of *H. pomatia*, but most of these efforts failed. Ligaszewski et al. (2007, 2014, 2016) showed that such conservation projects are only successful, if refuge habitats are available and if the local plant communities have a beneficial composition for *H. pomatia* (Ligaszewski et al., 2014). Due to the long lifespan from 8 to 35 years and the limited dispersal ability of the species, individuals will occupy same space throughout their life (Animal Base University of Göttingen, 2021). Observations and experiments show a precise memory related to topographical features of the hibernating area and snails return to hibernation areas utilized in previous years (Lind, 1988). Those findings highlight the need for temporal continuity of the habitat. The dispersal distance of *H. pomatia* after the last glacial period has covered approximately 560 km in 1700–2700 years. This results in an average rate of 330–200 m yr<sup>-1</sup>, similar to or slower than that of most tree species or other terrestrial snail species such as *Cepaea nemoralis* (Korábek et al., 2018). The future population status of *H. pomatia* therefore depends on habitats that are stable and protected. Invasive plant species are an additional threat, as for example the introduction of *Fallopia japonica* can lead to a decline of 85% of the population size in an affected area (Stoll et al., 2012). In summary, it can be said, that *Helix pomatia* still is of least concern in most European countries and can be found quite often. Possibilities to ensure its status have been found to a small extend and the snail will still play an active role in its ecosystem for the coming decades.

## 1.4 Research objectives

It is evident that a better understanding of the ecology of terrestrial gastropod species is needed to stop or at least slow down the current extinction dynamics and to increase the public awareness of its protection. The protection of biodiversity and simultaneously the protection of agricultural productivity can only be successful if species preferences and threat to their presence are understood.

Due to the existing knowledge gaps regarding the ecological importance of terrestrial gastropods, it is fundamentally important to collect data about the natural pressure by predators, the role as habitat for other species and their preferences for food resources. In this regard, this thesis addresses the following objectives:

1. Understanding the pressure through predators and parasitoids that attack *Helix pomatia* in its natural environment and how pressure relates to morphological traits of shells.
2. Understanding the use of *H. pomatia* shells by other species and the contribution of *H. pomatia* to the composition of invertebrate communities.
3. Understanding food preferences of *H. pomatia* and how these are influenced by environmental factors.

## II. General methods

### 2.1. The study area- Sachsendorfer Wiesen

The study area “Sachsendorfer Wiesen” is a low moor landscapes and a special habitat in the region of Brandenburg. They are located southwest of Cottbus and belong to the landscape protection area (LPA) "Meadow and pond landscape Kolkwitz-Hänchen"(Cottbus Administration, 2019). This area was officially designated a landscape conservation area by the Cottbus district and the Spree-Neisse district in May 1968 (Authority for Environment Brandenburg). For a precise definition of the term "landscape protection area", the Federal Agency for Nature Conservation (BfN) refers to the Federal Nature Conservation Act (BNatSchG). Section 26 (1) BNatSchG stipulates that “a special protection of nature and landscape is required” within a landscape protection area (Federal Agency for Nature Conservation, 2021).

1. "To maintain, develop or restore the performance and functionality of the ecosystem or the ability to regenerate and sustainably use natural resources,
2. because of the diversity, uniqueness and beauty or the special cultural and historical significance of the landscape or
3. because of their special importance for recreation."

The main protected objects of this landscape protection area include the habitats of site-specific plant and animal species, as well as the preservation of the landscape character.

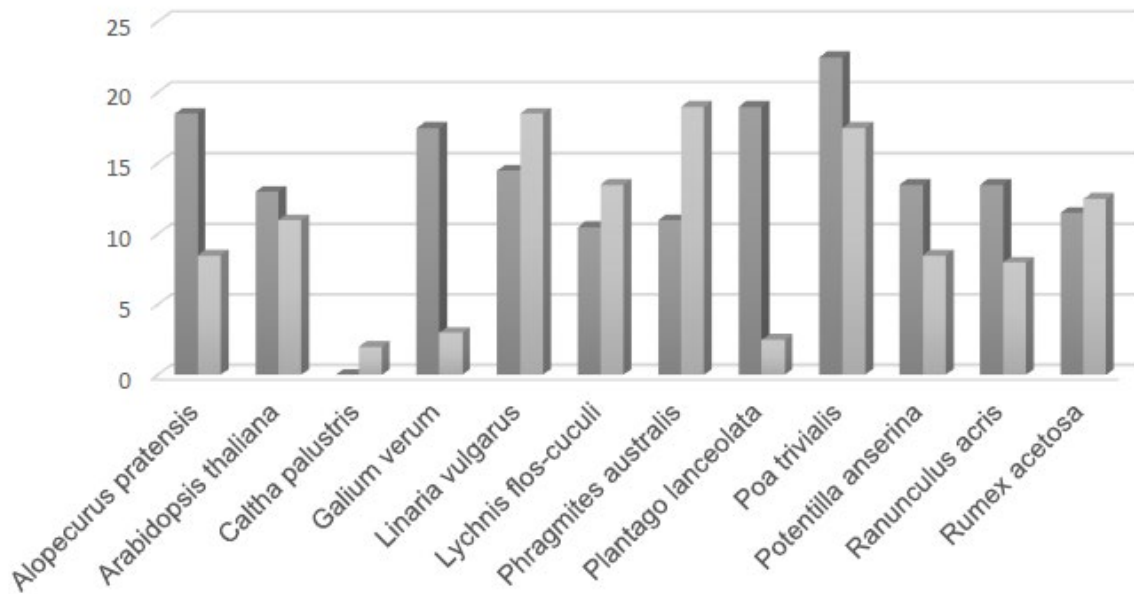
The “Sachsendorfer Wiesen” area is divided by the regional train connection Cottbus – Dresden into an eastern (district of Sachsendorf) and a western part (Klein-Ströbitz). The “Sachsendorfer Wiesen” are bordered by the district of Sachsendorf in the south and by the Priorgraben (a small creek) in the north. In total, it covers an area of 350 ha. In the western section, the terrain is at an altitude of 67 m normal height null (NHN) and in the eastern section at 70 m NHN (Wollmann, 2002). This low moor landscape has its origins in the Saale glaciation, where the wide, flat Baruth Urstromtal was formed. At that time, the “Sachsendorfer Wiesen” were a flow-through lake, which developed into a low moor due to gradual swamping (Keidel et al., 2009). This is also the reason for the presence of peat deposits, which are up to several meters thick (Wollmann, 2002). Over time, the area was made usable by humans by means of drainage and clearing. This resulted in many drainage ditches, which are still present today (Keidel et al., 2009). Figure 4 shows a typical view of the “Sachsendorfer Wiesen”.

The study area is used for recreational activities and the meadows are used to produce hay and silage for livestock. A first mowing takes place after Pentecost, which is used to produce hay, while the second mowing in late summer is used for silage. In rare cases a third mowing is possible in October (Hörnig, 2019).

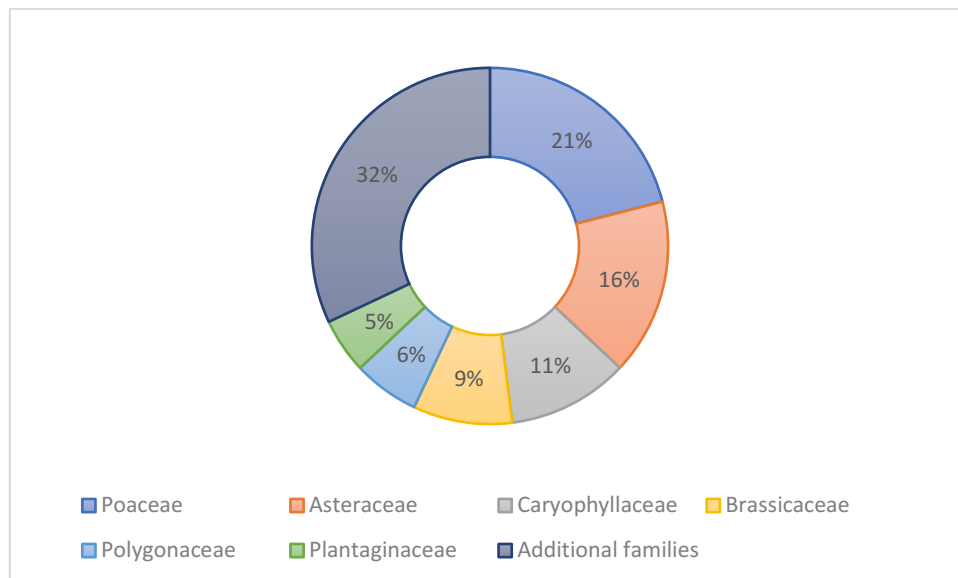


*Figure 4 Typical view of the Sachsendorfer Wiesen in spring, (Hoppe 2019)*

In the year 2000 a first botanical survey determined all plants species in the area and their frequency (Wollmann, 2002). Twenty years after this initial survey two additional surveys in 2019 and 2021 were used for comparison (Hoppe, 2019; Kahl, 2022). Figure 5 shows the difference in abundance for selected plant species between 2001 and 2019 and figure 6 the dominance of plant families in the Sachsendorfer Wiesen.



**Figure 5** Comparison of selected plant species between 2001 (light grey) and 2019 (dark grey) and their abundance in the study area. (Kahl, 2022)



**Figure 6** Overview of the most common plant families within Sachsendorfer Wiesen. Additional families: two species of each family are present: Apiaceae, Cyperaceae, Juncaceae, Lamiaceae, Ranunculaceae, Rosaceae, Rubiaceae (Kahl, 2022)

## 2.2. The study population and subpopulations of *Helix pomatia*

Eight subpopulations of *H. pomatia* were observed, which are separated through human settlements, train tracks, roads or larger meadow areas that isolate subpopulations from each other. Three of them are not inside the Sachsendorfer Wiesen area but very close.

Subpopulation P1 occurs in the West of the study area around a small hill, that was formerly used as a landfill. Next to it a big patch of *U. dioica* can be found as well as deciduous trees. The soil pH is 5.36. *Fallopia japonica* (Houtt) invades this area seriously and reduces the patch of *Urtica dioica*.

In the East of P1 subpopulation P2 can be found, which is completely covered by deciduous trees and free of *Fallopia japonica*. The main problem in this area is *Lamium galeobdolon* (Crantz), which is investing a high part of this area. The population density is far lesser than in P1 and the pH value is 6,87.

With the form of a triangle subpopulation P3 borders on two sides with a street and a railway station, while the third site borders on a meadow, where mowing is done twice a. A big patch of *Urtica dioica* can be found in this area and the population density is one among the highest in this study. Human intervention in this area is very limited and the pH value is 5,68.

Subpopulation P4 is the smallest one, as it is only covering 500 m<sup>2</sup>. Situated under a big tree and surrounded by bushes, garden waste is entered often, and the surrounding meadow is mowed twice per year. The density is very low and every year, less snails could be found. *Urtica dioica* is present in small numbers and the pH value is 5,12.

Subpopulation P5 directly borders on two estates and a high number of garages, which can be rented for personal use. On the other side a train road is situated, where the attached green space is managed by the German train service (DB). A high number of *Urtica dioica* can be found and garden waste is entered regularly. A lot of waste can be found, and the pH value is 6,48.

Directly at the western side of the train road, surrounded by garden plots and a street subpopulation P6 can be found. This area is officially a public space of the municipality of Cottbus, but gardeners start to use it in their own interest, building large places for their compost and planting cherry and peach trees as well as pumpkins. To avoid snail attack, the spread of molluscicides is done in certain areas and the pH value is 6,25.

Subpopulation P7 is in the East of the study area close to a football place. Only a small area is used for bulky waste, which caused a fire once. *Fallopia japonica* and *Lamium galeobdolon* have started to grow here as well and slowly take over. The population density of *Helix pomatia* in this area is the lowest compared to others and big patches of *Urtica dioica* are limited. Snails in this area are nearly as big as in P1 and P2 and the pH is quite good with 6,56.

The last population, subpopulation P8 is located directly between two train roads. Access for the public is not allowed as it belongs to the German train service. It is completely covered by deciduous trees, with a hill in the middle. *Urtica dioica* can be seen there regularly and no signs of garbage or *Fallopia japonica* and *Lamium galeobdolon* could be found. At this place *Lucilla scintilla* was found as well as the continuous present of wild bees. The pH value of this area is 5,52.

## 2.3. Study methods

Within my study I used different methods to achieve the above-mentioned objectives.

Chapter III analyses the predation pressure on *Helix pomatia* and its connection to morphological traits and the pH-value.

To start the research, the study area Sachsendorfer Wiesen was checked thoroughly for any signs of living *H. pomatia* and its whereabouts were marked on a map. Habitats of this species, that were separated by streets, train rails, human settlements or meadows were considered as different subpopulations. By this, eight subpopulations within and close to the study area were identified.

To determine the predation pressure 642 empty *H. pomatia* shells were sampled between 28 September 2016 and 30 November 2017. The number of shells per subpopulation ranged between 34–166 and depended on the habitat size and number of available shells. Estimates of morphometric traits may be biased towards larger, more conspicuous shells, and attack and utilization marks may result from interactions after the snail already died.

Out of the total 642 shells that were sampled for external attack marks, a random subsample of 353 shells was opened and checked for internal utilization marks by Diptera pupae. This was done in the laboratory, where we used needle-nose pliers to open shells from the aperture around the columella up to the apex. All marks indicating attacks on the outside of the shell were



recorded in the category “external attack”. Only shells with marks indicating the presence of Diptera pupae (preserved pupae or black marks on the inside of the shell indicating attachment points of pupae) were considered for the category internal utilization mark.

To estimate subpopulation densities, I counted all living individuals in spring 2017 and spring 2018 within an area of 9 m<sup>2</sup> at three locations in each subpopulation. This approach was optimized for a standardized sampling of subregions in each subpopulation to derive reliable estimates of population sizes of living snails.

The following morphometric traits were recorded from all subpopulations. The average mass of snails with shell was calculated on-site in each subpopulation by weighting living snails with a CS digital scale in April 2017 after hibernation. This was done per subpopulation for a minimum of 30 randomly selected snails per subpopulation to result in an average total mass of snails per subpopulation (hereafter “ $mass_{total}$ ”).

Between autumn 2016 and spring 2017 a minimum of 30 empty shells were collected in each subpopulation and weighed resulting in the average total mass (in g) of shells per subpopulation (hereafter “ $mass_{shell}$ ”). The average mass of shells ( $mass_{shell}$ ) was then subtracted from the average mass of snails in each subpopulation ( $mass_{total}$ ) to provide an estimate of the mass of snail bodies without shells per subpopulation (hereafter “ $mass_{body}$ ”; Sepúlveda et al., 2012).

In all subpopulations we measured 30 to 100 shells for shell height and width (in mm) with a sliding calliper. Shell volume (hereafter “ $volume_{shell}$ ”) was calculated for these shells by filling empty shells with sand and by then measuring the volume of sand per shell. Body density was mostly measured among aquatic gastropods in order to determine vulnerability regarding earthquakes or predators (Baums et al., 2003; Seike et al., 2019; Steward and McHenry, 2010), but this has not been addressed in terrestrial snails. Due to state laws considering the protection of *H. pomatia*, we needed to use a non-destructive method to calculate the quotient of the average body mass without shell ( $mass_{body}$ ) and the average volume of shells ( $volume_{shell}$ ) in each subpopulation.

To measure local soil pH, 76 soil samples were taken from the upper 10 cm across the subpopulations. Depending on the area size for each subpopulation two to six soil samples were taken, and the average soil pH was calculated for each area. Soil pH was measured using the Microprocessor-Präzisions-pH/mV-Meter pH 539 (Wissenschaftliche-Technische-Werkstätten GmbH) and 0.01M CaCl<sub>2</sub>. The soil sample was taken from the upper 10 cm as *Helix pomatia* is primarily in contact with this soil layer.

Chapter IV analyses snail shells as a microhabitat and research was done to identify local species that use shells of *H. pomatia* as a microhabitat. Therefore, 1408 empty shells of *H. pomatia* were ordered from a commercial snail farm (Walter Goller, 72525 Münsingen) for placement in those subpopulations (Tluste et al., 2020). Each provided shell was marked with a small point of gold paint 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. 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. To define the dominant vegetation a wooden frame of 1 m<sup>2</sup> 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). In each of the 16 study areas, 44 shells were placed in an area of 2 m<sup>2</sup>, with no specific distance or pattern between shells. The study areas showed no signs of frequent disturbance by humans.

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 as 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). 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.

Chapter V investigates the preferred food plants of *H. pomatia*. Each subpopulation was visited monthly to observe the snails' feeding behaviour from April to October 2021. All visits took place approximately one hour after sunrise, as this made observations possible without using a torch or flashlight, which could have disturbed snails and altered their feeding behaviour. All subpopulations were individually observed for 90 minutes during each visit with this survey time being stopped for the duration of each recording of feeding observation details. Due to the length of the survey in each subpopulation, it was not possible to visit more than one subpopulation on the same day. As habitats of the subpopulations were rather small (500 m<sup>2</sup> to 5000 m<sup>2</sup>) surveys covered the whole subpopulation area in a none standardized route, which avoided the destruction of the vegetation and the double counting of snails. Feeding observations for individuals were verified by observing the movements of the snails head - in relation to food resources. If movements of the mouth were observed or food passed through the digestive tract (visible through the skin) observations were verified and recorded. Observations of snails on plants, without indications of feeding activity, were not recorded. After recording the food resource (plant species, plant litter, or deadwood) a measurement tape was used to measure the height in the vegetation at which snails were observed, and sliding callipers were used to measure the height and width of snail shells. The number of whorls was recorded for each shell to determine the age classifying snails in their first year (1–3.5 whorls) and older snails (3.75 whorls or more) (according to Kiliyas, (2014) and Nordsieck (2022)). The level of shading of *H. pomatia* individuals, was recorded for each feeding observation as “full shade” (no direct sunlight (0), /fluctuation between shade and sunlight (temporarily in sunlight) or as no shade (permanent exposure to sunlight light).

Feeding observations on plant litter were also recorded. To record the plant communities in each subpopulation area, five to ten linear transects were performed in each area until no new plant species were recorded along the next transect. Plant species was determined for each feeding observation using the mobile application Flora incognita (Mäder et al., 2021) and Spohn et al., 2008 as mentioned before.

## Chapter III.- Morphometric traits of shells determine external attack and internal utilization marks in the Roman snail in eastern

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Contribution: Concept and development of the research objectives, design of the study, data collection and writing of manuscript

**Abstract.** Overexploitation, habitat destruction and a changing climate threaten populations of the Roman snail (*Helix pomatia* Linnaeus, 1758), which has led to a high protection status in Germany. Vertebrate and invertebrate predators, including parasites and facultative parasitoids, further cause pressure on populations. Given the conservation concern for *H. pomatia* and its rarity in the study region (Cottbus, Germany), we studied how predators and facultative parasitoids utilize *H. pomatia* shells with a focus on non-invasive field methods. As previous studies indicated that shell size may affect prey selection by predators, morphometric traits were measured in eight subpopulations. We identified the total number and percentage of *H. pomatia* shells that showed external attack marks by predators and internal utilization marks by Diptera pupae and related those utilization patterns to the morphometric traits of shells. A large proportion of the shells in local subpopulations showed signs of external attack and internal utilization, and both utilization forms were positively correlated. External attacks by predators were more frequent in larger shells and internal utilization by Diptera was more common in shells with higher body density. These results suggest a considerable pressure by predators and potential facultative parasitoids on *H. pomatia* populations in the study area. Future research should focus on the relationship between snails from the family Helicidae and flies from the genus *Discomyza*. Conservation programmes should consider abiotic habitat conditions together with potential trophic interactions to maximize the success of conservation strategies.

## Introduction

The Roman snail (*Helix pomatia* Linnaeus, 1758) is of considerable commercial interest as human food (also called “edible snail”; Bloszyk et al., 2010; Gheoca, 2013) and in medical research (Dwek et al., 2001). Exploitation by humans is a potential cause for population declines (Welch and Pollard, 1975; Andreev, 2006), especially as the species has a relatively slow reproduction and maturation rate (Ligaszewski et al., 2014) and long dormancy periods (Lind, 1989). Nevertheless, habitat destruction (Andreev, 2006) and a changing climate (Nicolai and Ansart, 2017) may threaten *H. pomatia* populations in the future as well, particularly in areas with unfavourable soil conditions. Those conservation concerns resulted in the development of breeding programmes to protect the species (Hardouin, 1995; Ligaszewski et al., 2014). National and EU-level regulations address overexploitation by creating different protection categories (Bouchet et al., 1999; Ligaszewski et al., 2016). National regulations protect *H. pomatia* in Germany (Bundesartenschutzverordnung (BArtSchV) Paragraph 1 Satz 1) and control the collection of snails, but they do not implement specific conservation programmes. The study area, in the Federal State of Brandenburg has a continental, dry climate with a limited presence of calcareous soils which both contribute to the rarity of the species and through this increase its conservation value. A citizen science project coordinated by the Nature and Biodiversity Conservation Union focuses on the identification of remaining habitats of *H. pomatia* and highlights the public awareness for the conservation of this species in the study region (NABU, 2019).

In addition to human exploitation, habitat management and climatic fluctuations, pressure from natural enemies may further affect populations of *H. pomatia*. Birds (e.g. *Coracias garrulus* Linnaeus (European roller) and *Phasianus colchicus* Linnaeus (pheasant)), rodents (e.g. *Apodemus sylvaticus* (Linnaeus) (wood mouse) or *Rattus rattus* (Linnaeus) (black rat)), reptiles (e.g. *Anguis fragilis* Linnaeus, 1758 (slow worm)) and ground beetles (e.g. Cychrus species) feed on *H. pomatia* (Coupland and Barker, 2004). Cychrus species even have morphological adaptations to their mouth parts to allow them to attack and consume snails (Digweed, 1993), but other, more opportunistic predaceous ground beetle species also attack terrestrial snails (Laroche, 1990). Several Diptera species (e.g. *Fannia canicularis* (Linnaeus), *Sarcophaga (Myorhina) nigrivantris*, *Chaetopleurophora bohemanni* or *Spiniphora bergenstammi*) may act as facultative parasitoids of *H. pomatia* (Barker et al., 2004). For other Diptera species, information is less well known or conflicting. For example, *Discomyza* species, like *D. incurva*,

breed in dead snails (Ferrar, 1987; Zatwarnicki and Mathis, 2007) and have been considered as parasites of *H. pomatia* for a long time (von Bergenstamm, 1864). Previous studies from Europe describe the occurrence of *D. incurva* in snail shells as rare or did not find this species in shells (Beaver, 1977; Buck et al., 2006).

Very little is known about population-level effects of predation on terrestrial snails (Millar and Waite, 1999), but even less is known about selection of prey or host snails by predators or parasitoids (Vermeij, 1995). Natural enemies of terrestrial snails often leave marks on the shell, either through external attack marks damaging the shell or internal utilization marks by larvae of pupae. Only two previous studies have used these marks to contribute to a better understanding of predation on terrestrial snails: Millar and Waite (2004) recorded patterns of shell damage in an English woodland and Němec and Horsák (2019) recently compared the identity of predator groups causing marks on the shells of the steppe snail *Granaria frumentum* (Draparnaud, 1801). Predation at the population level affects morphometric traits of shells (e.g. shell size; Goodfriend, 1986), and larger shells may even suggest a selective advantage against future predation (Liew and Schilthuizen, 2014). Shell size also affects predation, as for example smaller individuals of *Cepaea nemoralis* (Linnaeus, 1758) are more frequently attacked by beetles than larger individuals (Oosterhoff, 1977). Birds, for example song thrushes, showed preferences for larger shell sizes in the same species, but prey choice also depended on the different morphs in this snail species (reviewed in Goodfriend, 1986). Simultaneously considering external attack and internal utilization marks on snail shells together with morphometric shell traits will therefore contribute to a better understanding of attack and utilization patterns in *H. pomatia* populations.

Given the conservation concern for *H. pomatia* and its rarity in the study region, this field study focused on an improved understanding of how predators and facultative parasitoids utilize *H. pomatia*, with a focus on non-invasive field methods. We identified the number and percentage of *H. pomatia* shells that showed external attack marks by predators and internal utilization marks by Diptera pupae. To understand drivers of attack and utilization patterns, we measured morphometric traits of shells and related them to the observed proportion of marks in local subpopulations. We hypothesize that larger snail shells are more vulnerable to external attacks of predators due to a higher visibility but that the proportion of internal utilization marks by Diptera pupae is independent of morphometric traits.

## Material and methods

### *Study area and snail sampling*

The study area “Sachsendorfer Wiesen” is part of an approximately 350 ha large nature conservation area in Cottbus, Germany (Wollmann, 2002). After previous intensive agricultural use, the area has been managed as an amenity grassland since 1991. The single management practice is mowing, and the cutting frequency is once or twice a year. The vegetation in the area is dominated by *Urtica dioica* L. (common nettle), *Aegopodium podagraria* L. (ground elder) and *Chelidonium majus* L. (greater celandine).

The municipality of Cottbus gave permission to perform this research, under the conditions that no individuals of *H. pomatia* will be harmed and that areas that have been designated for the protection of the bird species *Crex crex* (Linnaeus, 1758) (corn crake) will not be entered.

We selected eight subpopulations of *H. pomatia* with a minimum distance of 30m and physical barriers such as by railway tracks or buildings between them. Prior to the sampling of shells, the whole study area was carefully surveyed for the presence of *H. pomatia* individuals and subpopulation habitats were selected based on their isolation from nearby habitat patches. Between 28 September 2016 and 30 November 2017, the same researcher sampled 642 empty *H. pomatia* shells (range of shells per subpopulation 34–166; Table 2) for examination of external attack marks by predators or internal utilization marks by Diptera pupae. Visual search for empty shells is a non-destructive sampling technique, which is a key priority for studies of protected species. This approach across the subpopulation area was optimized for the collection of a high number of empty shells across the subpopulation area. However, estimates of morphometric traits may be biased towards larger, more conspicuous shells, and attack and utilization marks may result from interactions after the snail already died. To estimate subpopulation densities, we visually counted all living individuals in spring 2017 and spring 2018 within an area of 9 m<sup>2</sup> at three locations in each subpopulation. This approach was optimized for a standardized sampling of subregions in each subpopulation to derive reliable estimates of population sizes of living snails. Live individuals of the protected species *H. pomatia* were not sampled or killed during this study.

### *Utilization marks*

Out of the total 642 shells that were sampled for external attack marks, a random subsample of 353 shells was opened and checked for internal utilization marks by Diptera pupae. This was done in the laboratory, where we used needle-nose pliers to open shells from the aperture around the columella up to the apex. All marks indicating attacks on the outside of the shell were recorded in the category “external attack” (Fig. 1a). Note that these marks are not equivalent to predation records, as the cause of mortality remains unknown and as marks could result from post-mortem attacks. External damage to shells by larger mammals is very unlikely, as the area is not visited by wild boars and as visits from other larger mammals are extremely rare due to the close proximity to human infrastructure and settlements. Only shells with marks indicating the presence of Diptera pupae (preserved pupae or black marks on the inside of the shell indicating attachment points of pupae) were considered for the category internal utilization mark (Fig. 1b and c). *Discomyza incurva* (Fallén, 1823), as a common species found in shells in this study, have larvae that are known to feed on decaying *H. pomatia* (von Bergenstamm, 1864; Sequey, 1934). It is unknown whether this species attacks living snails or primarily deposits eggs on snail carcasses (Kofler and Mildner, 2004), and internal marks cannot be differentiated between predation or scavenging events.

### *Morphometric traits and soil pH*

The following morphometric traits were recorded from all subpopulations. The average mass of snails with shell was calculated on-site in each subpopulation by weighting living snails with a CS digital scale in April 2017 after hibernation. This was done per subpopulation for a minimum of 30 randomly selected snails per subpopulation to result in an average total mass of snails per subpopulation (hereafter 149 “ $mass_{total}$ ”). Between autumn 2016 and spring 2017 a minimum of 30 empty shells were collected in each subpopulation and weighed resulting in the average total mass (in g) of shells per subpopulation (hereafter “ $mass_{shell}$ ”). The average mass of shells ( $mass_{shell}$ ) was then subtracted from the average mass of snails in each subpopulation ( $mass_{total}$ ) to provide an estimate of the mass of snail bodies without shells per subpopulation (hereafter “ $mass_{body}$ ”; Sepúlveda et al., 2012). In all subpopulations we measured 30 to 100 shells for shell height and width (in mm) with a sliding calliper. Shell volume (hereafter “ $volume_{shell}$ ”) was calculated for these shells by filling empty shells with sand and by then measuring the volume of sand per shell. Body density was mostly



measured among aquatic gastropods in order to determine vulnerability regarding earthquakes or predators (Baums et al., 2003; Seike et al., 2019; Steward and McHenry, 2010), but this has not been addressed in terrestrial snails. Due to state laws considering the protection of *H. pomatia*, we needed to use a non-destructive method to calculate the quotient of the average body mass without shell ( $mass_{body}$ ) and the average volume of shells ( $volume_{shell}$ ) in each subpopulation.

To measure local soil pH, 76 soil samples were taken from the upper 10 cm across the subpopulations. Depending on the area size for each subpopulation two to six soil samples were taken, and the average soil pH was calculated for each area. Soil pH was measured using the Microprocessor-Präzisions-pH/mV-Meter pH 539 (Wissenschaftliche-Technische-Werkstätten GmbH) and 0.01M CaCl<sub>2</sub>. The soil sample was taken from the upper 10 cm as *Helix pomatia* is primarily in contact with this soil layer.

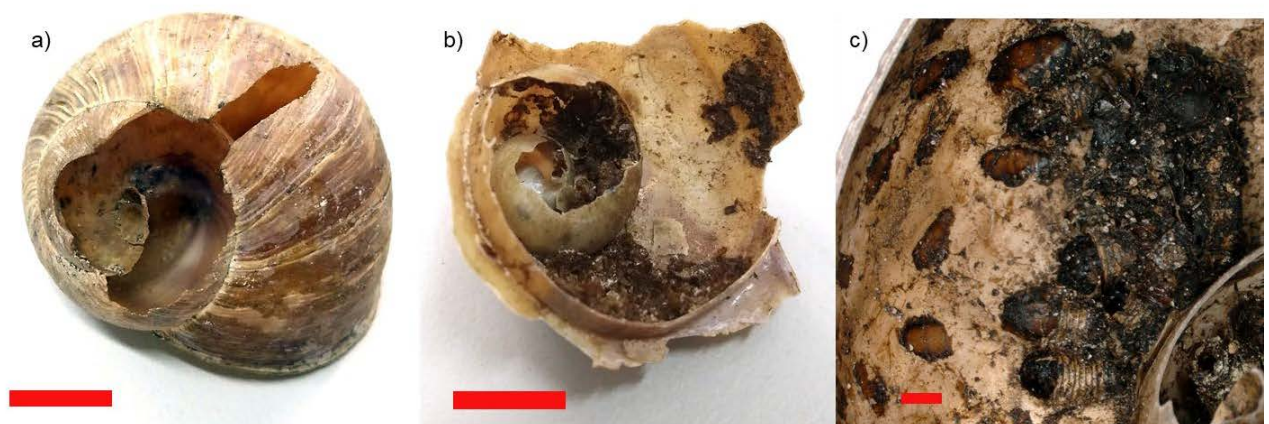
### *Statistical analyses*

Regression analyses were performed with distance-based linear models (DistLMs), an approach which can use non-Euclidean resemblance measures and derives p values from permutations (Legendre and Anderson, 1999; McArdle and Anderson, 2001). This approach has the advantages of allowing for internal standardization if predictor variables are not measured on the same scale (e.g., different morphometric traits like height in mm and mass in g) and relaxes the assumption that errors have to be normally distributed (Anderson et al., 2008). To test for the effect of soil pH, the percentage of internal utilization or external attack marks and the number of pupae on subpopulation size, we independently related these four predictors to the local estimate of snail density with DistLM. To find the best model predicting the variation in all four considered morphometric traits, we related soil pH, the percentage of internal utilization or external marks, and the number of pupae per shell as predictor variables to a resemblance matrix based on a multivariate dataset including the width (mm), height (mm), mass with (g) and without shell (g), and body density ratio in a single multiple multivariate regression model. We used Gower distances to generate a resemblance matrix of snail subpopulations to internally standardize for the different measurement scales of morphometric traits. The best model in this multiple, multivariate regression approach was selected based on data on from subpopulations (N D 8) and the AICc (version of Akaike information criterion with correction for small sample sizes). criteria for small sample sizes from all models with all possible predictor combinations.

Models within 21 AICc units of the best model are considered in the results section. All p values were based on 9999 permutations. Correlation analyses were performed using Pearson correlations. Principle coordinates ordination (PCO) illustrates the relationships between morphometric traits and predictors in an unconstrained ordination. All statistical analyses were performed with Primer v7.0 and the PERMANOVA add-on.

**Table 1** The estimated subpopulation size, total number of shells examined (= number of shells examined for external attack marks), percentage of shells with external attack marks, subset of shells examined for internal utilization marks, and percentage of shells with internal utilization marks. The final column shows the mean number of pupae observed per shell with internal utilization marks  $\pm$  standard error of the mean.

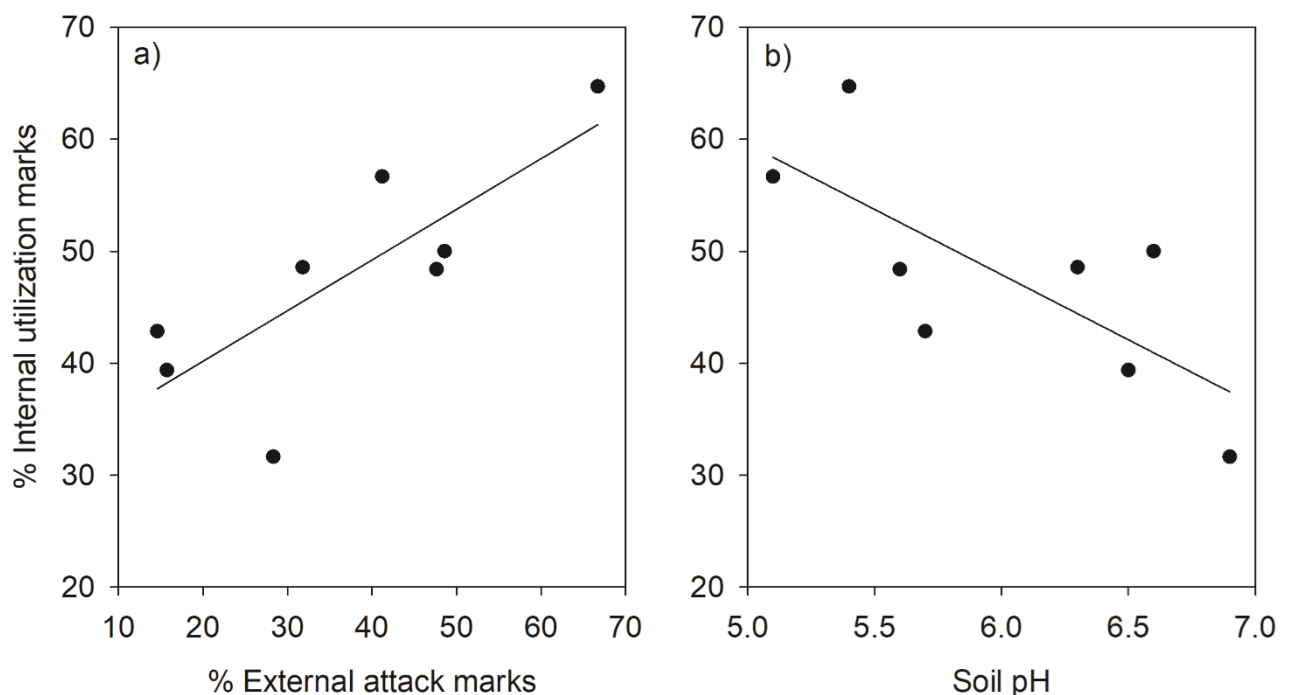
Subpopulation	Subpopulation size	No. shells external	% external	No. shells internal	% internal	Mean pupae per shell
1	2736	63	66.7	34	64.7	16.5 $\pm$ 4.6
2	2025	166	28.3	79	34.3	23.1 $\pm$ 6.7
3	2793	144	14.6	77	48.6	25.1 $\pm$ 5.9
4	163	51	41.2	30	56.7	21.2 $\pm$ 4.8
5	1695	34	15.7	33	39.4	13.4 $\pm$ 3.4
6	1553	107	31.8	35	48.6	11.3 $\pm$ 2.9
7	268	35	48.6	34	50.0	16.4 $\pm$ 3.3
8	2228	42	47.6	31	48.4	6.4 $\pm$ 2.0



**Figure 1** *Helix pomatia* shells with a) external attack marks (bird attack), b) internal utilization marks from Diptera pupae and c) details of internal utilization marks with Diptera pupae. The scale bar shows 1 cm in a) and b) and 1 mm in c)

## Results

The average estimated density of snails across the subpopulations was  $0.4 \pm 0.1$  (mean  $\pm$  SD) individuals per square metre. Out of 642 shells of *H. pomatia* analysed for external attack marks, 207 (32 %) showed signs of external attacks (Table 1). Out of 353 shells analysed for marks of internal utilization by Diptera pupae, 159 (45 %) showed such signs. The percentage of shells with external attack and internal utilization marks correlated significantly across subpopulations (Fig. 2a,  $R = 0.79$ ;  $p = 0.020$ ). The percentage of internal utilization marks further significantly correlated to the local soil pH across subpopulations (Fig. 2b,  $R = -0.74$ ;  $p = 0.036$ ). Other correlations between soil pH, percentage of internal utilization and external attack marks, and average number of pupae per shell were not significant ( $p > 0.05$ ).

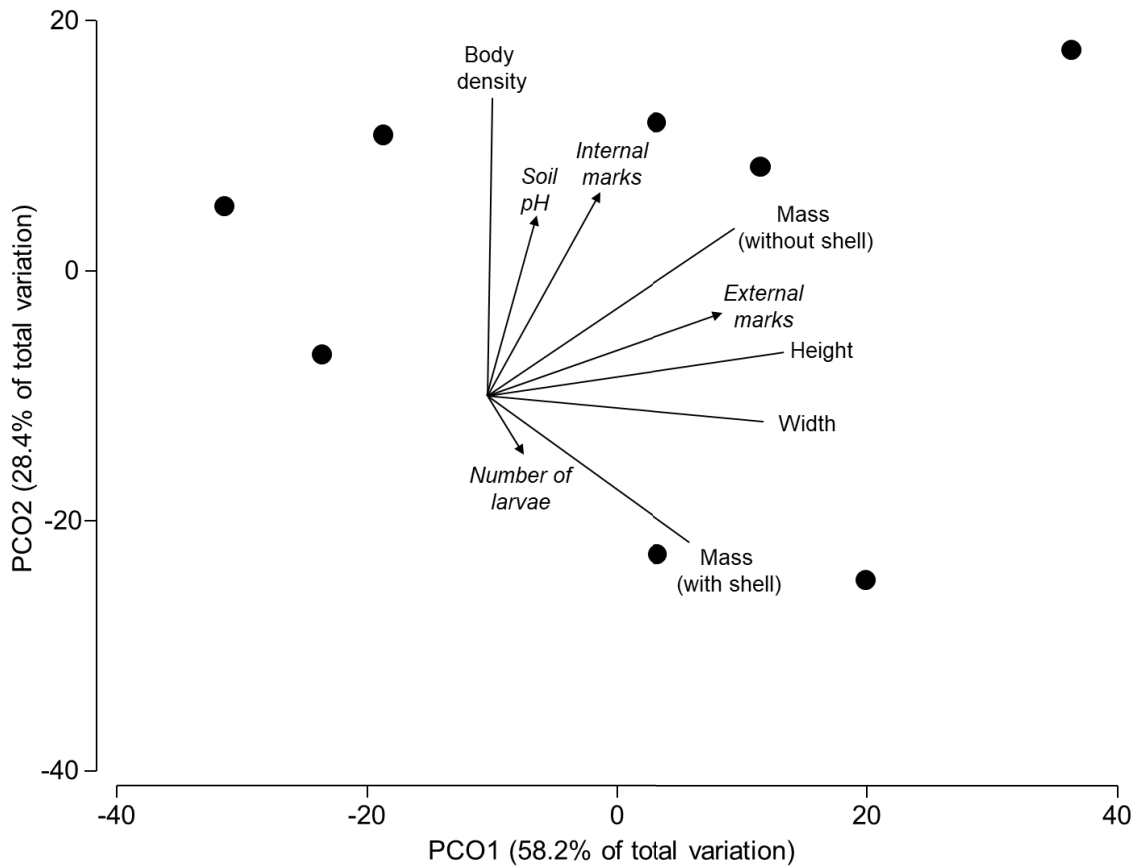


**Figure 2** Relationship between internal utilization marks and a) external attack marks and b) soil pH in shells of *Helix pomatia* in the studied subpopulations (N=8). Note that a single shell could show external attack and internal utilization marks.

The correlation of local density of snails per subpopulation was not significant to soil pH ( $R^2 = 0.39$ ;  $p = 0.108$ ) or the percentage of internal ( $R^2 = 0.04$ ;  $p = 0.410$ ), external attack marks ( $R^2 = 0.04$ ;  $p = 0.637$ ) nor to the average number of pupae per attacked shell ( $R^2 = 0.06$ ;  $p = 0.555$ ).

In total, 49% of all analysed shells contained pupae and the average number of pupae per shell was  $18.0 \pm 1.9$  (Table 1). The best model to predict the variation in the analysed morphometric traits included the percentage of external attack marks as single significant predictor (AICc= 56.5;  $R^2 = 0.35$ ;  $p = 0.039$ ), with one alternative model within 21AICc units (internal utilization marks only: AICc= 58.07;  $R^2 = 0.21$ ;  $p = 0.219$ ). Both soil pH ( $R^2 = 0.06$ ;  $p = 0.794$ ) and the average number of pupae per shell ( $R^2 = 0.03$ ;  $p = 0.911$ ) did not significantly affect the morphometric traits of shells. The ordination shows that most of the overall variation in all morphometric traits was explained by the individual variation in size (height and mass in Fig. 3) of shells (axis 1= 58.2 %) and body density (axis 2= 28.4 %). Larger shells had more external attack marks, and shells with higher body density had more internal utilization marks (Fig. 3).

Among the vertebrate predators in the study area, *Turdus philomelos*, *Turdus merula* Linnaeus, 1758 and *Pica pica* (Linnaeus, 1758) were most frequently observed. Arvicolinae and *Natrix natrix* (Linnaeus, 1758) were also present, but restricted to certain areas.



**Figure 3** Principle coordinates ordination based on a resemblance matrix (Gower distances) from morphometric traits (shell height [mm] and width [mm], shell mass [g], mass without shell [g] and body density [mass:volume ratio]) in the studied subpopulations. Vectors for morphometric traits (without arrow) and predictors (with arrow: soil pH, % internal utilization and external attack marks) were superimposed based on Pearson correlations with axis scores of the individual subpopulations.

## Discussion

A large proportion of the shells in local subpopulations showed signs of external attack (207 of 642 shells) and internal utilization (159 of 353 shells), and both utilization forms were positively correlated. Larger shells were more prone to external attack, and a higher body density resulted in more frequent internal utilization by Diptera. These results suggest a considerable pressure on *H. pomatia* by predators and potential facultative parasitoids in the study area.

Previous studies suggest that terrestrial snails are often not an important component of vertebrate diets and more related to certain periods (Goodhart, 1958; Davies and Snow, 1965; Gruar et al., 2003). Amongst the potential vertebrate predators, we observed *T. philomelos*, *Turdus merula* (Linnaeus, 1758) and *Pica pica* (Linnaeus, 1758) to attack individuals of *H. pomatia* in the study area. *Turdus philomelos* may be a major predator of invertebrates in the study area, but snails account for less than 20% of the diet in this species, while other bird species incorporate even lower numbers of snails into their diet ( $\leq 5\%$ ; Krištin, 1992). Previous research showed that external predators prefer snails with bigger shells due to the investment of energy in handling and breaking snails (Zach, 1978; Rosin et al., 2011; Brodersen et al., 2002; Allen, 2004). Furthermore, most snails are nocturnal and hide during the day (South, 1992) and larger shells may be more conspicuous during daytime. This positive relationship between shell size and external attack rates on the shell may be most important for visual predators (e.g. birds), as smaller less visually oriented predators may rather prefer snail prey with smaller shells (e.g. Oosterhoff, 1977). The present study shows that subpopulations with larger shells have higher proportions of external attack marks than subpopulations with smaller shell size. High predation pressure can affect population dynamics in terrestrial snail species but does not necessarily lead to a decline in population size (Allen, 2004). Invertebrate species that attack snails from the outside may have different preferences. Several beetle species incorporate gastropods into their diet (Symondson, 2004) but prefer smaller and injured snails due to attraction by emitted mucus (Mead, 1961; Wheeler, 1987; Digweed, 1993).

Regarding internal utilization, a large proportion of shells showed internal utilization marks from Diptera pupae (mainly genus *Discomyza*). In this study, we observed a large number of pupae (up to 128) per shell and 45% of all analysed shells showed signs of utilization by *Discomyza* pupae. *Discomyza incurva* was previously considered as rare or recorded in low

numbers from snail shells (Drake, 2006; Hofer and Waitzbauer, 2000), an observation we could not confirm in this study. Buck et al. (2006) stated that *Discomyza* flies only have a limited impact on snail populations. Potential body density showed the strongest correlation with percentages of internal utilization marks per subpopulation, and a high body density may result in higher oviposition rates by female flies. A higher nutritional value in snails with higher body density could explain the observed relationship. Other studies already confirmed that female flies of the family Phoridae prefer protein-rich food (Coupland and Barker, 2004) and that the fecundity of female flies in the family Sciomyzidae depends on the quality of the food (Beaver, 1973; Knutson and Vala, 2002). However, it remains unknown to what extent *Discomyza incurva* attacks living snails or primarily feeds on snail carcasses. Future research in this area could focus on live samples of *Helix pomatia* and *Discomyza incurva* to study interactions between these species in the laboratory. Field observations should address the timing of attacks and the state of the snail/shell at times of attack by the fly.

Larvae from different Diptera species have different pH optima (Grunewald, 1976; Uutala, 1987; Arimoro et al., 2007). Manipulation of the pH value of food attractants for example considerably altered the number of attracted female fruit flies (Bateman and Morton, 1981; Epsky et al., 1993; Heath et al., 1994; Duyck et al., 2004). Regarding the observed positive relationship between soil pH and the percentage of internal utilization marks in this study, soil pH values may have indirectly affected the number of ovipositing female Diptera. Snails consume soil (Elmslie, 1998; Mensink and Henry, 2011), and the diet alters the mineral content of the body tissue (Ireland and Marigomez, 1992; Ademolu et al., 2004) with potential consequences for their vulnerability to female flies.

The present study documents a high potential predation pressure and a positive relationship between external attack and internal utilization marks in subpopulations of *H. pomatia* in unfavourable environmental conditions. Previous studies documented that protection of *H. pomatia* subpopulations against vertebrate predators can contribute to an increase of population sizes (Sherley et al., 1998; Neuweger et al., 2001). In such conservation programmes, it is important to consider that external predators prefer larger individuals. Predators may vacate a feeding site, as soon as large individuals are exploited, and the snail population may recover relatively quickly after major predator species vacated the area (Mead, 1979). As *H. pomatia* has one of the highest legal protection statuses in Germany, priority needs to be given to the protection of suitable habitats.

## Chapter IV- Shells of the Roman snail are important microhabitats for soil invertebrates

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Contribution: Concept and development of the research objectives, design of the study, data collection, writing of the manuscript

**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.



## 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 cooccurrence 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.

## **Materials and methods**

### *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. C1). 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 m<sup>2</sup> 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 m<sup>2</sup>, 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. C2). 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. C3). A high-resolution digital microscope (Keyence VHX-950F) was used to analyse shell content and to determine invertebrate individuals. *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.

## Results

### *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. 3). 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:  $2.5 \pm 6.0$  vs.  $1.7 \pm 2.3$ ; 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 ( $2.5 \pm 5.9$  vs.  $1.7 \pm 2.5$ ). 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 ( $1.4 \pm 1.3$ ) 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 adopher communities in the two sample periods (Autumn vs. Summer) and dominant vegetation types (Herbs vs. Trees) with N as total number of collected shells.

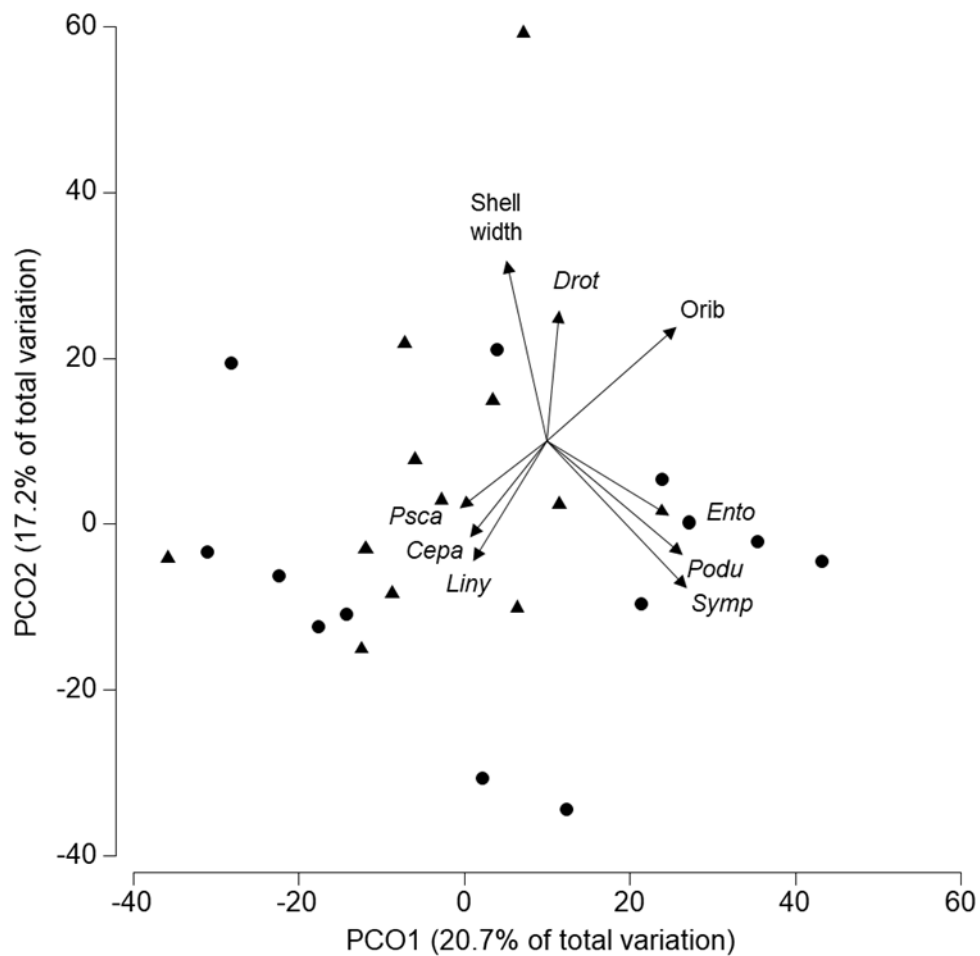
Taxon	Autumn (N=279)	Summer (N=339)	Herbs (N=354)	Trees (N=264)
Acari	99	155	203	51
Araneae	26	17	24	19
Chilopoda	1	0	1	0
Coleoptera	7	6	5	8
Collembola	138	298	356	80
Dermaptera	2	69	2	69
Diplopoda	5	18	14	9
Gastropoda	84	77	88	73
Heteroptera	11	4	10	5
Hymenoptera	5	16	8	13
Isopoda	91	188	166	113
Orthoptera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

#### *Taxonomic composition of shell adopher communities*

The composition of shell adopher 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 adopher 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 adopher communities (Tab. S2).

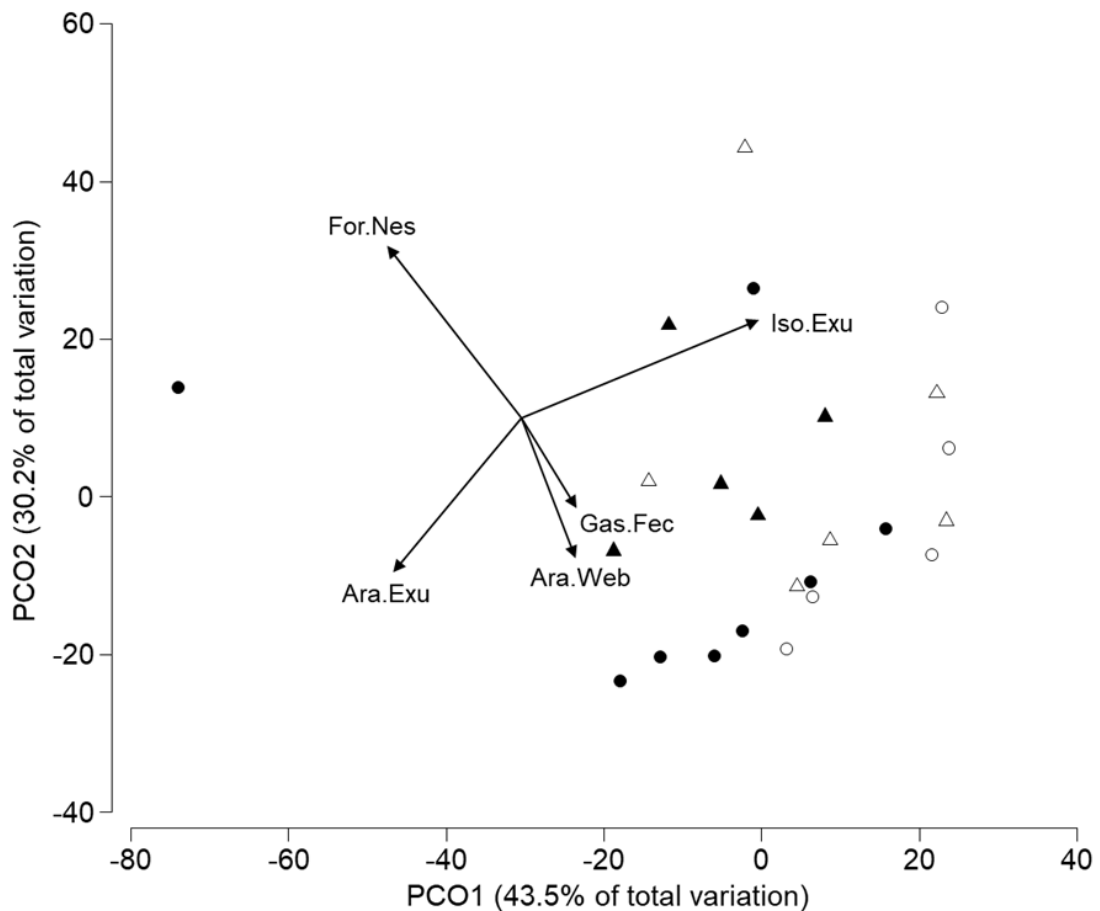
In this study, 26 % of all snail shells were colonized by isopods, of which 35 % of the shells showed signs of aggregation. This aggregation was not only observed between individuals of the same species, but also between individuals of different isopod species aggregating in the same shells. *Porcellio 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.

*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).



**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.



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).

### 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.

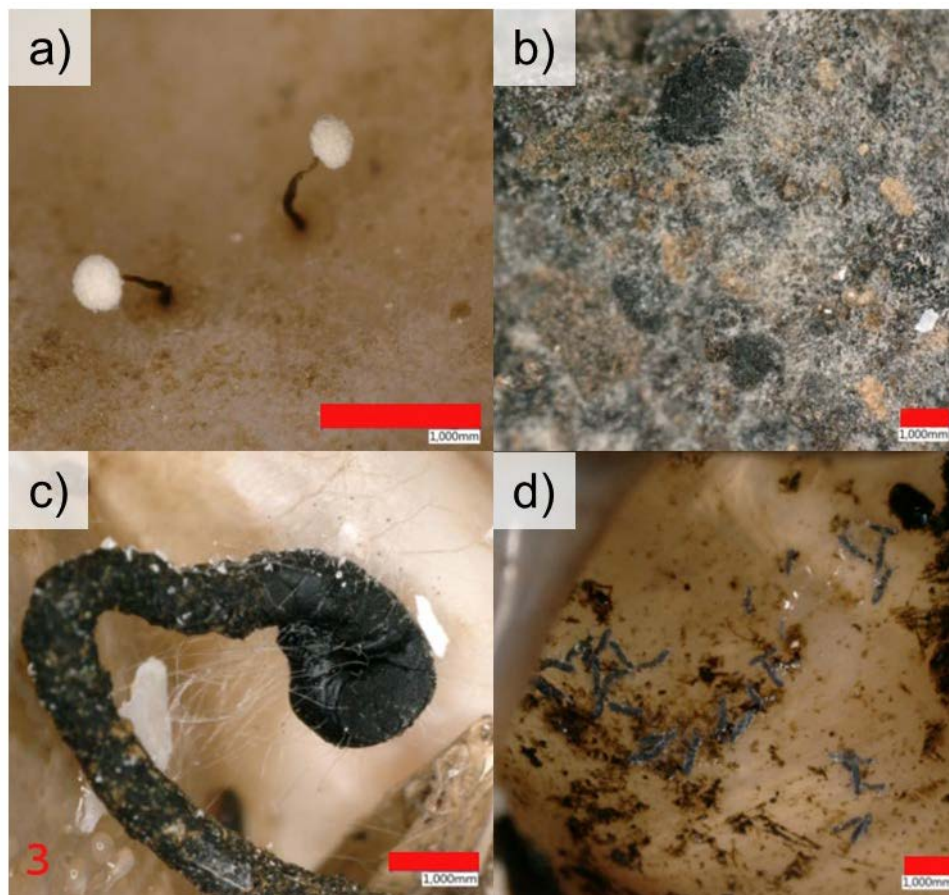
### *Number of shell adopters and taxonomic groups*

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.

### *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 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. 4 D).



**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.



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.



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

## **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.

## **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.

## Chapter V - The Roman snail (Gastropoda: Helicidae) is not a generalist herbivore, but shows food preferences for *Urtica dioica* and plant litter

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Contribution: Concept and development of the research objectives, design of the study, data collection, writing of the manuscript

**Abstract:** The food preferences and palatability of different plant species for snail and slug species in arable fields has been a major field of research in the past. The assumed diet of *Helix pomatia* (Linnaeus, 1758) however, provides an example of the limited knowledge of snail diets in non-agricultural habitats. This species has been described as a generalist herbivore, while showing preferences for individual plant species in another study. *Helix pomatia* is considered as a pest species, while also being a species that is listed as endangered in several Red Lists. In this study, the feeding activity of eight subpopulations of *H. pomatia* were recorded in a nature reserve in Cottbus, Germany from April to October 2021 to understand food preferences and feeding behaviour. Together with the plant species on which feeding was observed, the height of feeding in the vegetation, shell width and height, number of whorl, and exposure to direct sunlight at observation sites were recorded. Results indicate that *H. pomatia* preferences for *Urtica dioica*, and plant litter, which accounted for 35% and 44% of all observed feeding interactions respectively, as food resources, while generally only feeding on 27 of 143 available plant species. The importance of *U. dioica* as a food resource for 19 other terrestrial snail species is confirmed by 18 previous studies. In *H. pomatia*, analysis of the width and height of shells indicated that smaller, juvenile snails consumed plant material significantly higher in vegetation as compared to adult snails feeding closer to the ground. Awareness of the preference in *H. pomatia* for *U. dioica* as a food resource may be beneficial for land managers regarding the impact of this snail as an agriculture pest to crops. *Urtica dioica*, is a very important food plant for terrestrial snails, and could also play an important role in future species conservation strategies.

## Introduction

The palatability of different plant species and materials for snail and slug species in arable fields has been a major research field (Grime et al., 1968; Grime and Blythe, 1969; Dirzo, 1980; Briner and Frank, 1998; Iglesias and Castillejo, 1999; Brooks et al., 2003; Kozłowska and Kozłowski, 2009; Barlow et al., 2013). Speiser (2001) provides a comprehensive overview of the food resources and feeding behaviour of terrestrial snails and slugs. The planned introduction of weed species into arable fields or domestic gardens may cause a diet switch in terrestrial gastropods away from cultivated plants to such weeds as an alternative food resource (Airey, 1988; Cook et al., 1997; Frank and Friedli, 1999). However, less is known about food preferences of terrestrial gastropod species in non-agricultural ecosystems. Kiliás (2014), referring to laboratory experiments of Frömming (1950), describes the Roman Snail, *Helix pomatia* Linnaeus, 1758, as a generalist herbivore that selects food depending on the local density of plant species, with very limited avoidance of specific plant species. According to Kiliás (2014), plant litter is rarely consumed by *H. pomatia* and is only consumed in cases when fresh plant material is absent.

Terrestrial snail species of conservation concern (e.g., those on regional or national Red Lists) can locally act as pests of cultivated plants and adversely impact human interests. *Helix pomatia* is listed as a protected or endangered species in several European countries (Bruyne et al., 2003; Cuttelod et al., 2011; IUCN Red List, 2021) and its empty shells provide a valuable microhabitat for many soil-dwelling invertebrate species (Tluste and Birkhofer, 2021). However, *H. pomatia* is also known as agricultural pest in vegetable fields, crops, and ornamental plants (Port and Ester, 2002). In addition, *H. pomatia* populations in the wild are prone to overexploitation due to human food consumption, e.g., as in Moldavia and other East European countries (Welch & Pollard, 1975; Andreev, 2006). Considering these conflicting interests (pest control, species conservation, and overexploitation) it is surprising how limited our knowledge is about the feeding behaviour, natural history, and other preferences of this iconic snail species. In addition to the aforementioned descriptions of Killias (2014), Pollard (1975) investigated the activity of *H. pomatia* related to age and feeding in populations within Cambridgeshire, UK, observing that fresh plant material constituted their primary food source. Pollard (1975) also recorded 59 observations of *H. pomatia* feeding on dicotyledonous plants, including 42 observations of feeding on two species of the knapweeds, (*Centaurea scabiosa* and *Centaurea nigra*) in a population associated with chalk quarries in Cambridgeshire. These observations supported food preference independent of the local densities of other plant species, as previously proposed by Frömming (1950). Kiliás (2014) suggested that *H. pomatia* is a

generalist herbivore, primarily based on laboratory experiments. Pollard (1975), in contrast, proposed that *H. pomatia* has preferences for certain plant species, based on a small set of field observations. Given these conflicting definitions, there is a need for a systematic assessment of food selection in this species.

Food selection is a single dimension of feeding behaviour, as the selection of feeding habitats may also be affected by microclimatic preferences and predation risk. Terrestrial snails are prone to desiccation during feeding, as they are not fully protected by their shell (Attia, 2004). Hence, feeding while exposed to sunlight may constitute a risk of exposure to heat and other climatic stress, particularly in summer. Another major risk is predation, whether interspecific by a variety of vertebrate and invertebrate predators (Tluste et al., 2020), or intraspecific by predation of hatched individuals on eggs (Zajac and Kramarz, 2017). To understand the feeding ecology of *H. pomatia* in natural habitats, we recorded feeding events in eight subpopulations over a 7-month period in a nature reserve area (Cottbus, Germany). In addition to the presence and consumption of food plant species, we also recorded observations of *H. pomatia* feeding on plant litter and deadwood material, the size of the shells of all feeding individuals as an indicator of age, the feeding height of snails above ground, and the level of exposure to sunlight during feeding observations. We hypothesized that: i) *H. pomatia* is a generalist herbivore and feeds on most of the available plant species without any pronounced preferences, ii) a dominant proportion of the diet comprises live plant biomass while decaying plant material is not a major component of the diet, iii) larger and older individuals feed lower in the vegetation to be less exposed to predators and that iv) *H. pomatia* would actively avoid sunlight during feeding.



## Methods

### *Study area and measurements of the individuals*

The study area, known as “Sachsendorfer Wiesen”, is largely an amenity grassland and has been the location of previous studies of *H. pomatia* (Tluste et al., 2020; Tluste and Birkhofer, 2021). It is located southwest of Cottbus, East Germany and covers about 350 ha ( N 51°44′37.18, E 14°17′53.26). It is mainly managed by mowing and has been listed as a nature protection area since 1990. Sachsendorfer Wiesen also includes marsh areas, lakes, and several drainage channels, as well as deciduous and mixed patches of forest. For this study, eight subpopulations of *H. pomatia* were identified which were separated by meadows, railway tracks or human settlements. Each subpopulation was visited monthly to observe the feeding behaviour from April to October 2021. All visits took place approximately one hour after sunrise, as this made observations possible without using a torch or flashlight, which could have disturbed snails and altered their feeding behaviour. All subpopulation were individually observed for 90 minutes during each visit with this survey time being stopped for the duration of each recording of feeding observation details. Due to the length of the survey in each subpopulation, it was not possible to visit more than one subpopulation on the same day. As habitats of the subpopulations were rather small (500 m<sup>2</sup> to 5000 m<sup>2</sup>) surveys covered the whole subpopulation area in a none standardized route, which avoided the destruction of the vegetation and the double counting of snails. Feeding observations for individuals were verified by observing the movements of the snail head in relation to food resources. If movements of the mouth were observed or food passed through the digestive tract (visible through the skin) observations were verified and recorded. Observations of snails on plants, without indications of feeding activity, were not recorded. After recording the food resource (plant species, plant litter, or deadwood) a measurement tape was used to measure the height in the vegetation at which snails were observed, and sliding callipers were used to measure the height and width of snail shells. The number of whorls was recorded for each shell to determine the age classifying snails in their first year (1–3.5 whorls) and older snails (3.75 whorls or more) according to Kiliyas (2014) and Nordsieck (2022). The level of shading of *H. pomatia* individuals was recorded for each feeding observation as “full shade” (no direct sunlight), fluctuation between shade and sunlight (temporarily in sunlight) or as no shade (permanent exposure to sunlight light). The plant species was determined for each feeding observation using the mobile application *Flora incognita* (Spohn et al., 2008 and Mäder et al., 2021). Feeding observation on plant litter were also recorded. To record the plant communities in each subpopulation area,

five to ten linear transects were performed in each area until no new plant species were recorded along the next transect.

### *Statistical analysis*

To test for the individual (in marginal tests) and joint (in sequential tests) effect on diet composition by the predictor variables: 1) height in vegetation, 2) amount of shade, 3) sample day during the sampling campaign, 4) snail size (shell height and shell width), and 5) subpopulation (subpopulation 1–8), we used distance-based linear models (DistLM). Distance-based linear models are permutation-based multiple regression models that were developed to analyse multivariate community data as dependent variables (McArdle and Anderson 2001). The dependent data in our study were the average consumption of individual resources (which included all plant species and genera, plant litter, deadwood, and all individual snails own shells) by all snails in each subpopulation in a specific sample day. A table of 42 unique combinations between sample dates and subpopulations (8 subpopulations with 4–7 visits per subpopulation) and the proportional contribution of 29 consumed resources were transformed to a resemblance matrix showing all pairwise percentage similarities between the 42 combinations based on Bray-Curtis similarities. This resemblance matrix was then analysed with DistLMs based on a stepwise selection of predictors with Akaike information criterion (AIC) as selection criteria. All follow up analyses for pairwise relationships between single predictor variables and individual resources were tested with Spearman correlations. Rank-based Mantel tests were used to relate the average multivariate diet composition in each subpopulation over the whole study period to the composition of local plants communities and to the composition of only plants that were eaten across all subpopulations.

## Results

In total, 697 feeding observations were recorded, of which 246 (35%) were for *Urtica dioica* and 309 (44%) for plant litter resources, These two resources accounted for 79% of all records. Of the 143 plant species that were identified across all subpopulation areas, only 27 species were consumed by *H. pomatia*. In addition to plant-derived resources, five individual snails were observed feeding on their own shells, and one individual fed on a dead fly (order Diptera). Table S1 provides an overview of the number of plant species that were present in four (at least 50%) or more of the eight subpopulations but were never recorded as food for *H. pomatia* in this study. A total of 630 feeding events (90% of all observations) were recorded in full shade, 55 feeding event (8%) were recorded under fluctuating light conditions, and 12 feeding events (2%) were recorded in direct sunlight. The average feeding height in the vegetation of juvenile snails in their first year was significantly higher ( $384\text{mm} \pm 327\text{mm}$  standard deviation) compared to the feeding height of older snails ( $68\text{mm} \pm 194\text{mm}$ ) ( $F_{1, 695}=252.49$ ;  $P<0.001$ ).

The individual predictors feeding height in the vegetation, shell size and the identity of the subpopulation affected the diet composition of *H. pomatia* significantly in marginal tests, individually explaining between 26 to 28% of the variation in diet composition (Table 1a). In the sequential model, average shell size (Table 1b) explained 29.0% of variation as the first selected predictor. As the second and third selected predictors, average feeding height in the vegetation (7.8% of variation) and sample date (5.3% of variation) were selected and the three predictors together explained 42.2% of the variation in diet composition (Fig. 1). The fact that subpopulation explained 28.5% of the variation in the marginal tests (Table 1a but was not selected in the sequential model (Table 1b)) indicates that shell size was higher in some subpopulations across the sampling period. Indeed, subpopulation 2 had, on average, 1.2–1.7 times higher and 1.2–1.6 times wider shells compared to the other subpopulations.

The feeding proportions of the two resources correlating most with the predictors feeding height in the vegetation and shell width of snail subpopulations in the fitted model were *U. dioica* (feeding height) and plant litter (shell width, Fig. 1). Snail subpopulations with individuals feeding more on *U. dioica* were on average observed significantly higher in the vegetation, than snail subpopulations that on average fed less on *U. dioica* ( $R_s=0.82$ ;  $P<0.001$ ; Fig. 2a). Snail subpopulations feeding more on plant litter were observed lower in the vegetation than snail subpopulations that fed less on plant litter ( $R_s=-0.43$ ;  $P=0.004$ ; Fig. 2b). Snails in subpopulations with smaller individuals (shell width:  $R_s=-0.70$ ;  $P<0.001$ ; shell height:  $R_s=-0.68$ ;  $P<0.001$ ) fed more frequently on *U. dioica* (Fig. 3a,b). Snails in subpopulations with larger individuals (shell width:  $R_s=0.47$ ;  $P=0.002$ ; shell height:  $R_s=0.38$ ;  $P=0.013$ ) fed more

frequently on plant litter (Fig. 3c,d). The diet composition of *H. pomatia* subpopulations was not significantly related to the local composition of plant communities in each subpopulation area. This result was independent of the consideration of all the present plant species in a subpopulation area (Mantel  $R_S=0.04$ ;  $P=0.464$ ) or if only plant species were considered that were consumed across *H. pomatia* subpopulations in this study (Mantel  $R_S=0.29$ ;  $P=0.165$ ).

**Table 1** Distance-based linear models (DistLM) for the diet composition of *Helix pomatia* subpopulations. The individual predictor variables at the time of feeding observations are average feeding height of snails, shading category for snails and sample day. Indicator groups of predictor variables are shell size (average shell width and height), and subpopulation identity. DistLMs are given for predictors analysed individually and independent of each other in a) marginal models or analysed together to build the b) sequential model. The sequential model is based on the lowest AIC with pseudo-F values, P values, proportions of explained variation in diet composition and residual and regression degrees of freedom.

a) Marginal tests					
Predictor	Pseudo-F	P	Prop.	res. df	regr. df
Feeding height	13.72	<0.001	0.26	40	2
Shell size	7.97	<0.001	0.29	39	3
Shading %	1.23	0.267	0.03	40	2
Sample day	1.98	0.100	0.05	40	2
Subpopulation	1.94	0.015	0.28	34	8
b) Sequential					
Predictor	Pseudo-F	P	Prop.	res. df	regr. df
Shell size	7.97	<0.001	0.29	39	3
Feeding height	4.71	0.002	0.08	38	4
Sample day	3.45	0.010	0.05	37	5

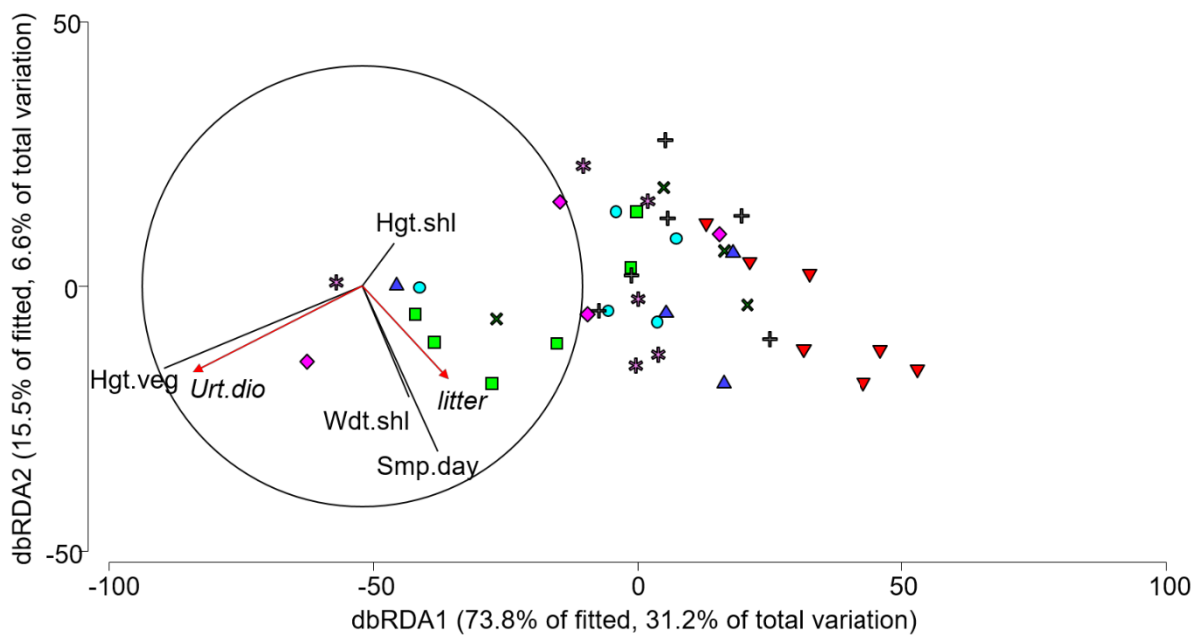
1 **Table 2.** Evidence from the literature for the crucial role of *Urtica dioica* as a preferred food plant of terrestrial snail species. The top section lists  
 2 references supporting the importance; the bottom section lists references finding no preference for *Urtica dioica*.

3

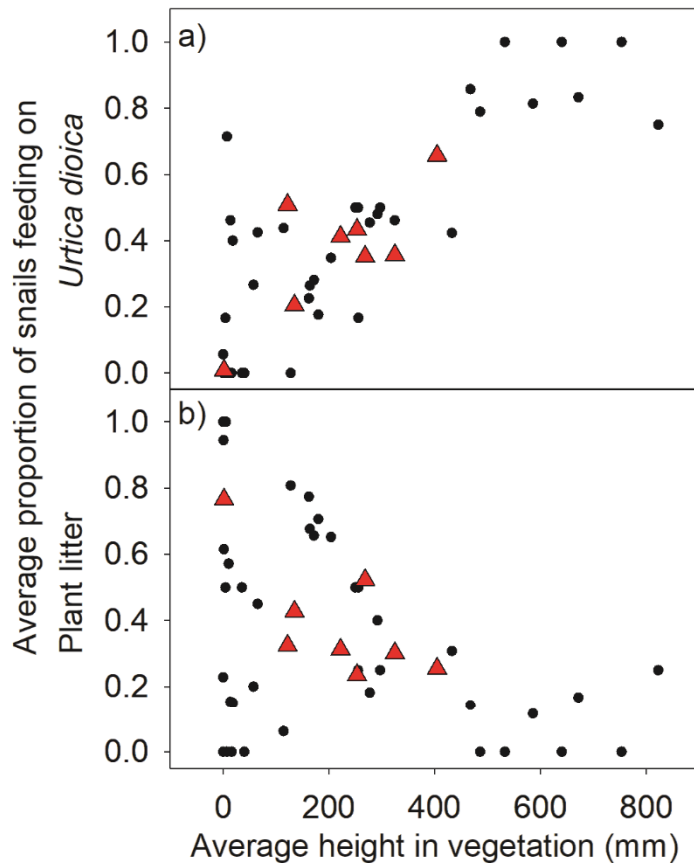
Snail species	Environment	Method	Observed preference	Reference
<i>Allogona townsendiana</i>	Field	Observations	<i>U. dioica</i> as important nesting ground and food source.	Steensma et al. 2009
<i>Ariolimax columbianus</i>	Laboratory	Choice experiment	<i>U. dioica</i> was highly preferred	Cates & Orians 1975
<i>Arion ater</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred with other species	Jennings & Barkham, 1975
<i>Arion ater</i>	Laboratory	Choice experiment	<i>U. dioica</i> was highly preferred	Cates et al. 1975
<i>Arion fasciatus</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> was highly preferred	Jennings & Barkham, 1975
<i>Arion hortensis</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred with other species	Jennings & Barkham, 1975
<i>Arion intermedius</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred with other species	Jennings & Barkham, 1975
<i>Arion subfuscus</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred with other species	Jennings & Barkham, 1975
<i>Bradybaena fruticum</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred	Hatzioannou et al. 1994
<i>Cepaea hortensis</i>	Field	Faecal analysis	47% of the faeces was <i>U. dioica</i>	Carter et al. 1979
<i>Cepaea nemoralis</i>	Field & Lab	Digestive tract & Choice experiment	<i>U. dioica</i> was highly preferred	Wolda et al. 1971
<i>Cepaea nemoralis</i>	Field	Faecal analysis	45% of the faeces was <i>U. dioica</i>	Carter et al. 1979
<i>Cepaea nemoralis</i>	Laboratory	Choice experiment	<i>U. dioica</i> among the most preferred plants	Grime et al. 1968
<i>Cepaea vindobonensis</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred	Hatzioannou et al. 1994
<i>Cornu aspersum</i>	Laboratory	Choice experiment	<i>U. dioica</i> preferred	Desbuquois & Daguzan 1995
<i>Cornu aspersum</i>	Field	Faecal analysis	25-65% of snails fed on <i>U. dioica</i>	Chevalier et al. 2001

<i>Cornu aspersum</i>	Field	Observations	50% of snails fed on <i>U. dioica</i>	Iglesias et al. 1999
<i>Cornu aspersum</i>	Laboratory	Olfactory influences	Prefers the smell of <i>U. dioica</i>	Dahirel et al. 2015
<i>Deroceras reticulatum</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred with other species	Jennings & Barkham, 1975
<i>Deroceras reticulatum</i>	Field & Lab	Choice experiment, Gut & Faecal analysis	24% of gut and faeces were <i>U. dioica</i>	Palant 1969
<i>Deroceras reticulatum</i>	Laboratory	Choice and no-choice experiment	After <i>Brassica napus</i> , <i>U. dioica</i> was the most preferred plant	Kozłowski & Kozłowska 2004
<i>Discus rotundatus</i>	Field	Faecal analysis, Food choice	Feeds on <i>U. dioica</i>	Mason 1970
<i>Hygromia striolata</i>	Field	Faecal analysis, Gut content	Feeds mainly on <i>U. dioica</i>	Chatfield, 1975
<i>Hygromia striolata</i>	Field	Faecal analysis, Food choice	Feeds on <i>U. dioica</i>	Mason 1970
<i>Monacha cantiana</i>	Field	Faecal analysis, Gut content	Feeds mainly on <i>U. dioica</i>	Chatfield, 1975
<i>Succinea putris</i>	Laboratory	Choice experiment	<i>Urtica</i> was highly preferred	Podroužková et al. 2015
<i>Urticicola umbrosus</i>	Laboratory	Choice experiment	<i>Urtica</i> was highly preferred	Podroužková et al. 2015
<i>Xeropicta arenosa</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> preferred	Hatzioannou et al. 1994

Species	Environment	Method	Observed preference	Reference
<i>Arion fasciatus</i>	Laboratory	Choice experiment	<i>U. dioica</i> was less preferred	Rathcke 1985
<i>Arion lusitanicus</i>	Laboratory	Choice experiment	<i>U. dioica</i> was less preferred	Briner & Frank 1998
<i>Arion lusitanicus</i>	Laboratory	Choice and no-choice experiment	<i>U. dioica</i> was less preferred	Kozłowski & Kozłowska 2004
<i>Arion subfuscus</i>	Laboratory	Choice experiment	<i>U. dioica</i> was less preferred	Rathcke 1985
<i>Arion rufus</i>	Laboratory	Choice and no-choice experiment	<i>U. dioica</i> was less preferred	Kozłowski & Kozłowska 2004
<i>Deroceras reticulatum</i>	Laboratory	Choice experiment	<i>U. dioica</i> was less preferred	Rathcke 1985
<i>Helix lucorum</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> not preferred	Hatzioannou et al. 1994
<i>Monacha cartusiana</i>	Field	Faecal analysis, Gut content	<i>U. dioica</i> not preferred	Chatfield, 1975
<i>Monacha cartusiana</i>	Field & Lab	Choice exp. & Faecal analysis	<i>U. dioica</i> not preferred	Hatzioannou et al. 1994

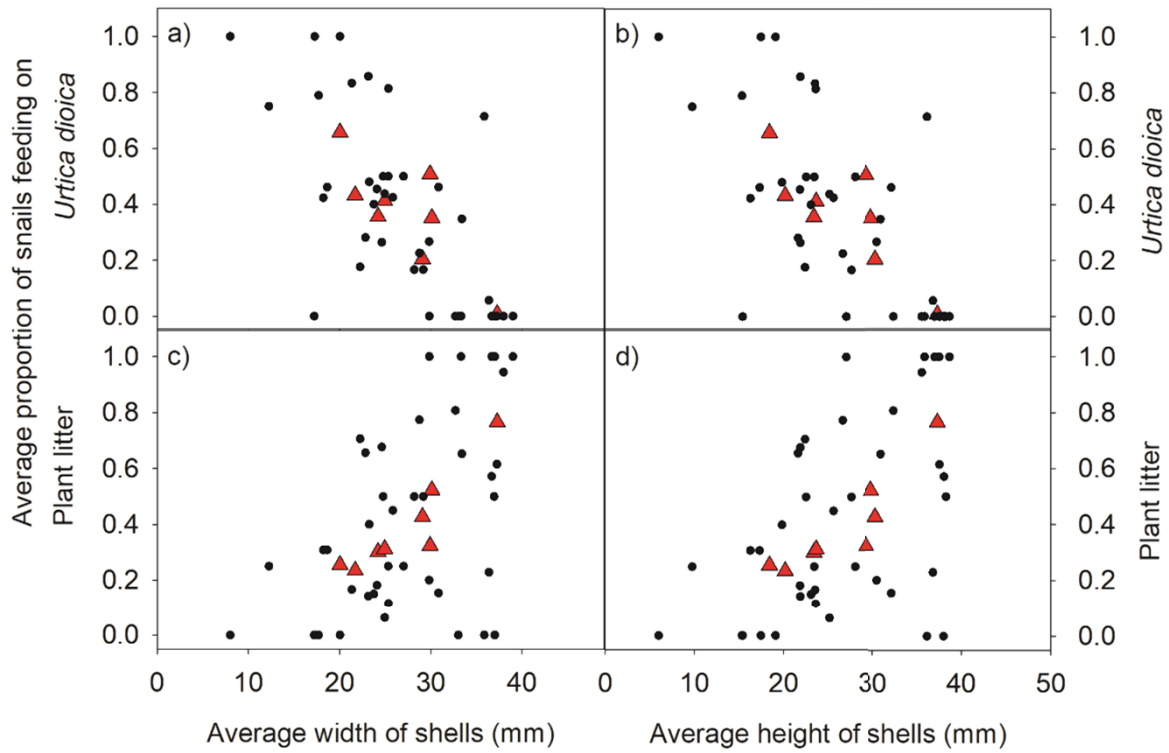


**Figure 1** Distance-based RDA plot showing the resemblance between *Helix pomatia* subpopulations based on the average diet composition of snails in different subpopulations and at different dates. Subpopulations 1–8 are indicated by different colours and symbols. Vectors are fitted for the predictor variables selected in the distance-based linear model (black: Hgt.shl, average shell height, Hgt.veg, average feeding height; Wdt.shl, average width of shells; Smp.day, sample day). Diet resources (in red with: Urt.dio, *Urtica dioica*; litter, plant litter) with multiple correlation coefficients  $>0.3$  are superimposed.



**Figure 2** Relationship between the average height of feeding snails in the vegetation per subpopulation independent of the sample date (▲) and for individual sample dates (●) and the average proportion of individuals feeding on a) *Urtica dioica* or b) plant litter.





**Figure 3** Relationship between the average width (a&c) and height (b&d) of snails shells per subpopulation independent of the sample date (▲) and for individual sample dates (●) and the average proportion of individuals feeding on a&b) *Urtica dioica* or c&d) plant litter.

## Discussion

The results indicate that *Helix pomatia* is not a generalist herbivore. Across the studied subpopulations, 35% of all feeding observations came from a single plant species, only 27 out of 143 plant species were consumed, and plant litter was a very important food resource even though fresh plant material was available throughout the study period. Results also indicate that shell size (as proxy of age) influenced the average feeding height in the vegetation. In addition, 90% of all feeding individuals were observed in full shade, while only 2% of all individuals feeding in full exposure to sunlight. Future research on feeding preference in this species should consider environmental factors such as humidity and differences in daytime temperature as well as the community composition and activity of potential competitors.

### *Food preferences*

Previous studies documented 19 terrestrial snail and slug species that, like *H. pomatia*, are also not generalist herbivores and preferred the common nettle, *U. dioica*, as food plant over other species. Only five out of 18 studies (Table 2) showed that terrestrial gastropods had no preference for food plants or had a preference for a different plant species (Table 2). *Deroceras reticulatum* (Müller, 1774) showed a preference for *U. dioica* in two studies (Jennings & Barkham, 1975; Palant, 1969), but a preference for a different plant species in a third study (Duval 1971). These findings highlight the importance of *U. dioica* as food plant for a wide range of terrestrial snail and slug species in Europe, and other regions where it was introduced and established itself. For example, in North America (Steensma et al., 2009; Edworthy et al., 2012) were *Allogona townsendiana* shows a high preference for *U. dioica* as a food source and a mating location. Dahirel et al. (2015) found that the terrestrial snail species *Cornu aspersum* (Müller, 1774) can perceive the presence of *U. dioica* from 40 cm distance and will actively move towards this plant. Considering the importance of *U. dioica* for terrestrial snails, it is surprising, that it has been rarely tested for commercial snail pest management (Jovanović et al., 2007). It could be promising to minimize snail pest damage using *U. dioica* as cover for vineyards and citrus orchards (Sakovich, 2002; Sanderson and Sirgel, 2002) or as plants for flower strips in vegetable gardens (Port and Ester, 2002). Freshly cut material of *U. dioica* may also be used as a bait to attract and remove snails from crops or to collect snails for consumption in regions with sufficiently large natural populations.

Litter decomposition contributes to nutrient cycling as an important ecosystem service in many terrestrial and aquatic ecosystems (Tresch et al., 2019; Richardson and Hanna, 2021). In total, 44% of all *H. pomatia* observations were made on snails feeding on litter. This indicates that the species, with its relatively large body size and locally high abundances, could be an important decomposer. Several studies highlight that mollusc species are important for aquatic litter decomposition by decreasing litter cellulose content and enhancing mobilization of nutrients (Schaller, 2013, Schmidt et al., 2015). Türke et al. (2018) showed, that the Apple Snail, *Pomacea canaliculata* (Lamarck, 1819) could contribute considerably to litter decomposition as an invasive species in rice paddies. Decomposition rates are positively related to the local biomass of snails, the shell size and to some extent to the shape of shells (Meyer III et al., 2013; Astor et al., 2015). The contribution of terrestrial snail species to ecosystem functions and services deserves more attention in future studies.

### *Feeding behaviour*

Grime and Blythe (1969) studied the climbing behaviour of the snail species *Arianta arbustorum* (Linnaeus, 1758). Older and larger individuals were less efficient climbers than younger and smaller individuals. In this study, younger and smaller individuals of *H. pomatia* were more commonly observed to feed higher up in the vegetation than older and larger individuals. There are at least three potential non-exclusive explanations for this observation: 1) the additional weight of the shell in larger individuals could reduce the ability to climb and persist higher in the vegetation, 2) larger snails are more prone to attacks by predators in general (Tluste et al. 2020) and may have a better chance to avoid attacks from the air or from mammal species if they hide lower in the vegetation, 3) terrestrial snails may have positive (*C. aspersum*) or negative (*H. pomatia*) phototaxis (Wilbur & Yonge, 1966; Zieger, 2008; Hussein et al., 2021) and this could be related to vegetation height. According to an owner of a *H. pomatia* snail farm, it is very easy to collect juvenile *H. pomatia* individuals by laying out white sheets of paper to which juvenile snails are attracted (pers. comm. A. Nicolai). Such behaviour could indicate positive phototaxis or consumption of paper material by the juvenile snails. On the contrary, Zieger (2008) states that adult *H. pomatia* prefer darker areas and orientate themselves towards black surfaces, indicating negative phototaxis. Pollard (1975) showed that the activity of snails strongly decreases with age, which could be related to the avoidance of light in older individuals. Further research is needed to understand this behaviour in snails of different age.

*Urtica dioica* is a very important food plant for terrestrial snails and could play an important role in the conservation of species. A high availability of patches of *U. dioica* increases food availability for *H. pomatia* and adds preferred hiding and breeding habitats. Due to the height and growth form of *U. dioica*, it also offers more shade primarily benefitting older individuals of *H. pomatia*. Litter resources are equally important for *H. pomatia* as they are frequently consumed by larger, potentially reproductive individuals. The contribution of snails to litter decomposition in grassland habitats deserves more research attention, as these organisms may be overlooked but important contributors to litter decomposition and local nutrient cycles.

**Geolocation information:** The study area is located at N 51°44'23.82 and E 14°18'13.83. In order to protect this species from exploitation the exact location of subpopulations will not be published openly.

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**Data availability statement:** The data will be uploaded on Research Gate after publication of the manuscript.

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## Chapter VI – General discussion

### 6.1. Linking results from chapter III-V within the ecological context

This research shows, that *H. pomatia* is an important link between primary producers and consumers across trophic levels. Within the Sachsendorfer Wiesen they are available as a food source for at least 30 different other species, that consume snails as a source of calcium (Allen, 2004; Barker & Efford, 2004, Gosler, 2006). Especially in areas as the Sachsendorfer Wiesen where the pH value is very low (4,6 – 6,27), snail shells can be crucial for birds as they have a higher demand for calcium in breeding seasons or fall (Dhondt and Hochachka, 2001; Taliaferro et al., 2001; Kwiecinski et al., 2019). Those findings highlight the importance of snails and especially the establishment of *Helix pomatia* within this area. Horsák (2009) mentioned the decline of molluscan species richness, together with a degradation of habitat. *Helix pomatia* is one of the biggest European snails and a generalist, while it lives in a broad range of habitats and close to human settlements (Wiese, 2016). This makes it an ideal species to fill up the gap that was left by other more specialist molluscan species. In relation this, only a single breeding program is known to me by Ligaszewski et al. (2014, 2016). Re-establishment of *H. pomatia* populations was possible in this program, with individuals being raised in a greenhouse and released back into the wild after a year. The effects on local populations were positive and had a positive influence on the populations age structure. Certain requirements were considered like the presence of hiding places and preferred food for the species. Considering the high predation pressure observed in this the study in Brandenburg the following result from Ligaszewski et al. (2005) is interesting: Within an experiment 77100 snail eggs were laid out within the greenhouse, of which only 4800 survived the first winter. Only 6.2 % of the eggs survived and this is approximately only four times higher than the number of adults that were used for breeding (N=1254) (Ligaszewski et al, 2005). Together with the calculated predation pressure, the number of snails surviving throughout the first 2-3 years till maturity was generally very low and it can be expected that breeding programs need to reinforce the population continuously over several years. Also, dispersal takes place easier as it is less dependent on certain habitat requirements (Dahirel, 2014). Still predation pressure will again greatly limit its survival rate and distribution (Yamanishi et al., 2012; Rietl, 2018; Saeki , 2020, Uehara, 2021)

Snail shells, especially of *H. pomatia* offer an important microhabitat for soil organisms as well as for wasps or bees (Moreno-Rueda et al., 2008; Müller et al., 2018; Bogusch et al., 2020; Romero et al., 2020). Ants, as for example *Temnothorax crassispinus*, can even close the shell with sand or other material, but movement of the shell resulting in damage of the entrance, will lead to an evacuation of the whole colony (Aleksiev, 2007; Mitrus, 2015; Mitrus, 2019). Unfortunately the simple present of snail shells alone is not enough to attract shell adopters (Bogusch et al., 2019) as weather and other unmeasured variables may influence the choice (Moreno-Rueda et al., 2008; Romero et a., 2020). Snail shells are very opportunistic microhabitats. They remain longer than tree ponds, but shorter than dead wood or dry stone walls (Manenti, 2014), by this bringing more heterogeneity into the ecosystem. Doblas-Miranda et al. (2009) found that heterogeneity of microhabitats and temporal variability on macroinvertebrate are important factors to a more dynamic interaction within the ecosystem. Microhabitats have extraordinary potential to buffer climate and likely reduce mortality during extreme climate events (Scheffers et al., 2014). In opposite to tree ponds and dead wood, shells are not always offering food at the same place and shell adopter leave their hiding place to find food. Oribatid mite communities in different microhabitats vary in abundance and body structure due to the availability of food, competition or other variables (Brückner et al., 2019). Also, among bees, shells are mostly used as a timely restricted breeding place (Müller et al., 2018). Considering all those different points, it can be said, that snail shells as a microhabitat offer a valuable addition to many ecosystems.

*Helix pomatia* has a pronounced preference for *Urtica dioica* and plant litter as food resources. By feeding on plant litter snails contribute to decomposition and nutrient cycles in the soil (Slim et al., 1997; Harris, 2008; Astor, 2015; Türke, 2018). Food preferences can greatly influence the spatial distribution of a species, as it was already confirmed for mammals and birds (Bennetts et al., 2006; Heroldová et al., 2008; Cho et al., 2020) Mostly preferences are connected to higher nutritional values of the preferred food (Cook et al., 2000; Suba et al., 2020) and have a direct impact in shaping an ecosystem (Kunz et al., 2011; Mikulka et al., 2018). Liang et al. (2018) for example could show, that the herbivory snail *Neohelix alleni* can have an impact on the tree seedlings within a forest and Motheral and Orrock (2010) suggest that the preferences of *Helix aspersa* (Müller) for certain types of grass may lead to the establishment of unpreferred grasses in natural communities. On the other side the interactions between plant and herbivory may also lead to an increased grow of preferred plants, as it was observed

between the snail *Littoraria irrorate* (Say) and the plant *Spartina alterniflora* (Loisel) (Zerebecki et al., 2017). Apple snails like *Pomacea* and *Asolene* are already banned from trade and transport within the EU, due to their huge impact on ecosystems (EFSA 2013 and 2014).

Considering the findings of Chapter III and the impact of predation pressure, we must understand, that *H. pomatia* is occupying very small areas within the Sachsendorfer Wiesen. This species is not able to occupy a big area, but has to concentrate on places, where no mowing takes place, no human intervention happens and that are free of *Sus scrofa*. In total it is occupying 0.66% of Sachsendorfer Wiesen. The effects of predator hunting mode on grassland ecosystems have been studied before (Schmitz, 2008) and can have a huge impact on the vegetation composition, also regarding snails (Griffin et al., 2011, Davidson et al., 2015). It needs to be assumed, that even *H. pomatia* shows preferences for certain plant types, these choices are still influenced by the limited access to other areas, due to human intervention and predation pressure. On the other hand, it would be interesting to find out, in which way the constant herbivore pressure of *H. pomatia* has an impact on the plant composition within the Sachsendorfer Wiesen. As this species is one of the biggest snail species in Europe, it also controls more resources than other snails in this area (Hausdorf, 2007).

In conclusion it can be said, that the role of *H. pomatia* within an ecosystem is as complex and important as that of every other species and a still a lot of research is necessary to understand it in detail.

## 6.2. Research gaps and recommendations

The results that internal utilization partly depends on the local soil pH as well as the fact that *U. dioica* is the preferred food plant species provide relevant insights for further investigation and experiments. The hypothesis that *H. pomatia* forms an important link between different species within the ecosystem and could be considered as ecosystem engineer is supported by this study.

The establishment of nature reserves in order to save the habitat of endangered species utilizing ecosystem engineers has been an option for future conservation strategies since a long time (Geldmann, 2013). However, a more general question is if protected areas contain most of the endangered species. Sólymos and Feher (2005) showed that the current nature reserves in Hungary did not overlap with Hotspots of the snail fauna. A comparison of their current locations even revealed that the number of rare species was 31 instead of the actual 16 and that 66% - 75% of their occupied areas were outside of protected areas (Sólymos, 2007). Horsák et al. (2017) observed the same problem in Czech Republic: calcareous forest areas act as a hotspot for the snail fauna, but mostly do not belong to protected areas. Those results indicate that new protection areas must be established to ensure conservation of terrestrial gastropods and all species that benefit from their presence, like predators or shell adopters. Carrizo et al. (2017) highlighted the need for a trans-frontier system to protect the freshwater biodiversity, this argument is not limited to areas aquatic ecosystems, as protected areas should connect terrestrial ecosystems across different countries.

Next to the questions of how and where to allocate protected areas, another question becomes more pressing: Which species do we prioritize for protection? Suggestions are made to concentrate on the concept of phylodiversity, which relates to saving a branch of the tree of life instead of all the branches (Laity et al., 2015). In the case of *H. pomatia*, it was decided in Germany to protect this species and to prohibit the collection of individuals in nature. Although the law is implemented, it will not protect the eight subpopulations from this study. Land-use change and transformation is the major threat for suitable local habitats and breeding programs can help to re-establish the species after it is locally extinct.



Bolam et al. (2022), evaluated the targets of the Post-2020 Global Biodiversity Framework, which are the following eight.

- (1) implement spatial planning to retain existing intact ecosystems
- (2) restore degraded ecosystems and ensure connectivity among them
- (3) conserve land and sea areas, especially areas of particular importance for biodiversity, through protected areas and other effective area-based conservation measures
- (4) ensure active management to enable species recovery, conserve genetic diversity, and reduce human–wildlife conflict
- (5) ensure that harvesting, trade, and use of species are legal, sustainable, and safe
- (6) prevent or reduce the introduction of invasive alien species, and (where introduced) control or eradicate them
- (7) reduce pollution
- (8) minimize the impact of climate change on biodiversity

Most of these targets can be related to the study area Sachsendorfer Wiesen and *H. pomatia* populations living there. An evidence-based planning is necessary to ensure protection and restoration of the habitat and conservation of those populations. Active management is required to reduce the density of invasive species and minimize pollution in this area. Only under such improved practices, the *H. pomatia* population will have a long-term perspective to survive at the Sachsendorfer Wiesen. Being more aware of the ecological importance of snails in local ecosystems and communicate this important role, for a species that most citizens previously heard about, offers a unique opportunity to improve habitat protection for otherwise not well-known soil organisms and biodiversity in general in Germany.

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## Appendix

**Table A 1** Overview of terrestrial snail and slug species that were found in the study area Sachsendorfer Wiesen and their Red List Status in Germany: Nb – not evaluated; \* - least concern; V – vulnerable; 3 – endangered; D – data deficient

Species	Red List Status (2012)
<i>Alinda biplicata</i> (Montagu 1803)	*
<i>Arianta arbustorum</i> (Linnaeus 1758)	*
<i>Arion vulgaris</i> (Moquin-Tandon 1855)	Nb
<i>Arion circumscriptus</i> (Johnston 1828)	*
<i>Arion intermedius</i> (Normand 1852)	*
<i>Arion distinctus</i> ( J. Mabille 1868)	*
<i>Arion fuscus</i> (O.F. Müller 1774)	*
<i>Cepaea nemoralis</i> (Linnaeus 1758)	*
<i>Cochlicopa lubrica</i> (O.F. Müller 1774)	*
<i>Discus rotundatus</i> (O.F. Müller 1774)	*
<i>Euconulus praticola</i> (Reinhardt 1883)	V
<i>Helix pomatia</i> (Linnaeus 1758)	*
<i>Limax maximus</i> (Linnaeus 1758)	*
<i>Lucilla scintilla</i> (R.T. Lowe 1852)	D
<i>Nesovitrea hammonis</i> (Ström 1756)	*

<i>Oxychilus cellarius</i> (O.F. Müller 1774)	*
<i>Oxychilus draparnaudi</i> (Beck 1837)	*
<i>Perforatella bidentata</i> (Gmelin 1791)	3
<i>Punctum pygmaeum</i> (Draparnaud 1801)	*
<i>Succinella oblonga</i> (Draparnaud 1801)	*
<i>Trochulus hispidius</i> (Linnaeus 1758)	*
<i>Truncatellina cylindrica</i> (A. Férussac 1807)	3
<i>Vallonia costata</i> (O.F. Müller 1774)	*
<i>Vallonia excentrica</i> (Sterki 1893)	*
<i>Vitrina pellucida</i> (O.F. Müller 1774)	*
<i>Vertigo substriata</i> (Jeffreys 1833)	3
<i>Zonitoides nitidus</i> (O.F. Müller 1774)	*

*Table A 2* 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
Apoidea	Apiformes	0	1	1	0	1
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
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	<i>Rhyparochromidae</i> 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

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*Table A 3 Dominant vegetation, latitude and longitude of 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 A 4** Overview of plant species, that have been present in four or more subpopulations, but were never consumed by *H. pomatia*.

Resource	Number of subpopulations present
<i>Acer platanoides</i>	4
<i>Alliaria petiolata</i>	4
<i>Ballota nigra</i>	5
<i>Capsella bursa-pastoris</i>	4
<i>Chelidonium majus</i>	8
<i>Corylus avellana</i>	4
<i>Galium mollugo</i>	5
<i>Geranium robertianum</i>	4
<i>Hypericum maculatum</i>	5
<i>Lamium album</i>	4
<i>Mahonia aquifolium</i>	5
<i>Prunus padus</i>	8
<i>Ranunculus ficaria</i>	4
<i>Sambucus</i> sp.	4
<i>Scilla siberica</i>	5
<i>Solidago canadensis</i>	5

**Table A 5** Overview of the plant species or material that was consumed during the observation period, together with the number of feeding observations and the subpopulations feeding was observed.

Plant eaten	Observations	Subpopulation							
		1	2	3	4	5	6	7	8
<i>Aegopodium podagraria</i>	12	X		X	X	X	X	X	
<i>Allium vineale</i>	19		X						
<i>Arctium lappa</i>	2							X	
<i>Crepis capillaris</i>	1					X			
<i>Galium aparine</i>	1	X	X	X		X	X	X	X
<i>Geum urbanum</i>	2	X	X			X	X	X	X
<i>Glechoma hederacea</i>	1			X	X	X		X	X
<i>Humulus lupulus</i>	16	X	X	X	X	X	X		X
<i>Lamium galeobdolon</i>	2	X	X	X		X		X	X
<i>Lamium purpureum</i>	1	X	X	X	X	X	X		X
<i>Lepidium draba</i>	1						X	X	
<i>Lunaria annua</i>	3		X	X		X	X		
<i>Muscari sp.</i>	1		X	X		X	X	X	
<i>Ornithogalum umbellatum</i>	8		X			X	X		X
<i>Poales sp.</i>	19	X	X	X	X	X	X	X	X
<i>Potentilla indica</i>	2	X					X		
<i>Robinia pseudoacacia Bark</i>	1	X	X	X		X	X		X
<i>Rubus sp.</i>	5	X	X			X	X	X	X
<i>Rumex acetosa</i>	1	X	X		X	X	X	X	
<i>Stellaria media</i>	8	X		X	X	X	X		X
<i>Taraxacum sect. Ruderalia</i>	3	X	X	X	X	X	X	X	
<i>Tulipa sp.</i>	2			X			X		
<i>Tussilago farfara</i>	1				X				
<i>Urtica dioica</i>	246	X	X	X	X	X	X	X	X
<i>Veronica hederifolia</i>	15	X	X	X	X	X	X	X	X
<i>Vicia hirsuta</i>	1					X			X
litter	309	X	X	X	X	X	X	X	X
dead wood	8	X	X	X	X	X	X	X	X
shell	5	X	X	X	X	X	X	X	X

**A9** Overview of mentored students and their work as a contribution to a better understanding of the study area Sachsendorfer Wiesen:

Engel, R. (2019) „Erfassung der Maulwurfsvorkommen im Untersuchungsgebiet Sachsendorfer Wiesen in Cottbus“, Bachelorthesis

Freybe, T. (2022) „Vergleich einzelner Parameter, im Ökosystem Sachsendorfer Wiesen, zum besseren Verständnis der Maulwurfpopulationen“, Masterthesis

Gatzke, S., Kretschmer, J., Travica, J. & Konetzny, J.(2020) „Die Beobachtung der Aktivität des europäischen Maulwurfs auf dem Untersuchungsgebiet Sachsendorfer Wiesen in Cottbus“, Study assignment

Glockmann, M. (2019) “Monitoring der Sachsendorfer Wiesen in Cottbus“, Study assignment

Hoppe, A. (2019) “Die Vegetation ausgewählter Bereiche in den Sachsendorfer Wiesen in Cottbus“, Bachelorthesis

Hörnig, E. (2019) „Management der Sachsendorfer Wiesen in Cottbus“, Study assignment

Kahl, S. (2022) „Vegetationsaufnahme und Vergleich einzelner Ausschnitte von Maulwurfsterritorien, im Ökosystem “Sachsendorfer Wiesen“ in Cottbus, zum besseren Verständnis der Maulwurfpopulationen“, Study assignment

Kleine, D. & Dziallas, J.C. (2020) „Talpa europaea - Untersuchung der Populationsentwicklung auf den "Sachsendorfer Wiesen" in "Cottbus" von 2018/19 zu 2019/20“, Study assignment

Kleine, D. (2022) „Bodenuntersuchungen auf zwei Waldflächen in Brandenburg (Deutschland) - Einschätzungen des Verhältnisses von pH-Wert, der Leitfähigkeit und dem Corg-Gehalt des Oberbodens zur darüber liegenden Vegetation“, Masterthesis

Roschig, E. (2021) „Korrigierte Maulwurfskartierung und vergleichende Analyse von Hügelmustern“, Bachelorthesis