Trophic niche size and overlap in temperate forest land snails are affected by their lifestyle and body size

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RECEIVED: 7 MAY 2022 | REVISED AND ACCEPTED: 7 SEPTEMBER 2022
EDITOR: DENIS COPILAS-CIOCIANU

Abstract

Land snails represent a large diversity of species in the forest floor. Some species prefer to stay in the leaf litter, while others like to climb up vegetation. They are considered generalist herbivores/decomposers. Although the exact trophic position of most species is often difficult to determine, a low rate of trophic niche partitioning within an assemblage is assumed. We compared isotopic niche sizes and overlaps between and within four local land snail assemblages using stable isotope Bayesian ellipses. We found significant differences in trophic niche size (expressed by corrected standard ellipse area) as a function of body size and lifestyle. We hypothesised that the larger niche size of smaller and/or arboreal snail species is due to their limited mobility and the presence of spatially structured food resources. In contrast, a broad and similar mixture of leaf litter sources results in a homogeneous diet for individuals of larger, highly mobile, epigean species, i.e., smaller niche size. We documented multiple overlaps of isotopic niches between species within an assemblage, although arboreal species exhibited slightly different niche positions, indicating specific diets. When comparing all pairwise combinations, we found that isotopic niches of species using different lifestyle did not overlap, in contrast to species using similar lifestyle. In addition, the trophic niches of opportunists with respect to lifestyle were intermediate between those of species from the outermost categories. Our results fit the general concept of variable and overlapping...
trophic niches in co-occurring snail species. However, we were able to demonstrate differences in species that rarely occupy the same microhabitat.

Keywords

body size – land snails – lifestyle – niche overlap – niche size – stable isotope analysis

Introduction

Forest soils represent a very complex environment with an enormous variety of life forms that encompass a huge biodiversity of organisms (Giller, 1996). Snails are one of them, serving as an important regulators of plant growth (Rees & Brown, 1992), and agents of decomposition processes (Theenhaus & Scheu, 1996; De Oliveira et al., 2010). In addition, they represent an easily available prey for a variety of higher-level consumers (Barker, 2004; Němec & Horsák, 2019). Although they are generally considered as herbivores and unspecialised opportunistic feeders with no clear food source preferences, their diet is still poorly understood, especially for minute snail species (Speiser, 2001). Additionally, some land snail species are carnivorous, mostly feeding on other snails and annelids (Barker & Efford, 2004).

Most species considerably differ in their lifestyle, as many species exclusively inhabit leaf litter and upper soil layer (Locasciulli & Boag, 1987), while others climb trees (Saeki et al., 2017) and rest in deadwood and under the bark (Kirchenbaur et al., 2017). Many species express rather opportunistic preferences, being commonly found at all types of microhabitats (Kemencei et al., 2014). It seems that differentiation in their microhabitat preferences is not driven to reduced interspecific competition among land snails, as it is generally negligible. Therefore, trophic niches are found to be highly overlapping as investigated using stable isotopes (Schmidt et al., 2004; Meyer & Yeung, 2011; Larson & Black, 2016; Bonkowski & Kappes, 2017; Němec et al., 2021), which is consistent with the finding of terrestrial communities showing high species overlap (Rossi et al., 2015). However, certain level of compartmentalisation has been documented for some gastropod species within an assemblage with respect to different trophic level (Meyer & Yeung, 2011), ontogenetic stage, utilisation of specific diet (Bonkowski & Kappes, 2017), or lifestyle (Saeki et al., 2017). In general, land snail trophic niche variation is largely unknown between populations of individual species, but also between local assemblages. Assuming snails are true opportunistic consumers, it would be naive to expect low or no trophic niche variation between local populations. Some early studies have indicated that trophic niches of land snails and slugs may vary depending on the qualitative and quantitative composition of food resources (Pallant, 1972; Hatzioannou et al., 1994; Iglesias & Castillejo, 1999).

It is known that the mobility of organisms is positively correlated with their body mass (Schmidt-Nielsen, 1972; Hirt et al., 2017), which has been well documented also for gastropods (Baur & Baur, 1988; Giokas & Mylonas, 2004; Honek & Martinkova, 2011; Dahirel et al., 2015). Given the heterogeneous nature of forest floor with a mixture of food sources, opportunistic lifestyle combined with greater mobility should provide more opportunities for exploration of the inhabited area. This could lead to a more heterogeneous
| Species              | Family             | Total no. individuals | Body size (mm³) | Lifestyle    | Mean $\text{SEA}_c$ per site |
|---------------------|--------------------|-----------------------|-----------------|--------------|-----------------------------|
| *Aegopinella nitidula* | Oxychilidae       | 10                    | 236             | Epigean      | 0.56                        |
| *Aegopinella ressmanni* | Oxychilidae       | 30                    | 506             | Epigean      | 1.52; 0.40; 0.53            |
| *Aegopis verticillus* | Zonitidae         | 5                     | 6283            | Epigean      | 0.48                        |
| *Alinda bicipita* | Clausiliidae       | 6                     | 162             | Oportunistic | 2.52                        |
| *Cepaea hortensis* | Helicidae          | 5                     | 3686            | Oportunistic | 1.15                        |
| *Cochlodina laminata* | Clausiliidae       | 6                     | 127             | Arboreal     | 6.81                        |
| *Ena montana*      | Enidae             | 18                    | 302             | Arboreal     | 3.97; 6.05                  |
| *Fruticicola fruticum* | Bradybaenidae     | 39                    | 3137            | Oportunistic | 0.55; 1.78; 0.96; 2.50      |
| *Helix pomatia*    | Helicidae          | 30                    | 21701           | Oportunistic | 1.66; 0.84; 1.43            |
| *Macrogastra ventricosa* | Clausiliidae     | 10                    | 125             | Arboreal     | 6.62; 0.45                  |
| *Monachoides incarnatus* | Hygromiidae       | 5                     | 1201            | Oportunistic | 0.49                        |
| *Oxyloma elegans* | Succineidae        | 10                    | 314             | Oportunistic | 9.99                        |
| *Succinea putris* | Succineidae        | 10                    | 414             | Oportunistic | 4.57                        |
| *Trochulus villosulus* | Hygromiidae       | 10                    | 265             | Oportunistic | 2.34                        |
| *Urticicola umbrosus* | Hygromiidae       | 30                    | 478             | Oportunistic | 3.23; 1.53; 2.57            |
| *Zonitoides nitidus* | Gastrodontidae     | 10                    | 87              | Epigean      | 4.42                        |
diets of land snails based on the use of variable foraging strategies at a given time. On the other hand, these specimens could selectively search for the most suitable diet sources.

To the best of our knowledge, there are no studies that have examined the position and size of land snail isotopic niches in relation to body size (here also representing mobility). It is known that saprotrophic invertebrates select their food (Hatzioannou et al., 1994; De Oliveira et al., 2010), but it is known that land snails have a broader food spectrum (Maraun et al., 2003). It remains poorly known whether certain preferences that might affect trophic niche characteristics are related to species’ body size. However, there is some evidence that body size of detritivores, particularly millipedes, can be related to feeding traits (Semenyuk & Tiunov, 2019). In predators, more homogeneous diets and smaller niches have been documented for species of larger body size (Zhao et al., 2014; Bašić & Britton, 2015; Pettitt-Wade et al., 2018). In contrast, Sanders et al. (2015) observed increases in niche size with increasing body size in several spider species, assuming that individuals can potentially consume a wider range of prey as the predator grows.

In this study, we aim to evaluate the partitioning of trophic niches among co-occurring land snail species using the isotopic signatures of 16 species from four local assemblages. As this is the first study conducted on land snails, and previous studies on other invertebrates showed ambiguous patterns with body size, we had no predictions regarding isotopic niches in relation to the species-specific traits tested. We asked whether the size and position of isotopic niches in land snails expressed by corrected standard ellipse area (SEAC), were related to lifestyle and body size of the species. We also tested whether differences in species-specific traits among the land snails predicted the percentage of overlap in SEAC for pairwise species combinations at each site. We hypothesise that the overlap will decrease as species differences increase.

Materials and methods

Data collection and sample processing

Samples were collected from three sites (A: 49.96846N, 16.37833E; B: 49.99910N, 16.33401E; and C: 50.00121N, 16.30257E), represented by semi-open floodplain forests situated in river alluvium along the Tichá Orlice River, Czech Republic. The sites were characterised by the presence of various trees such as linden (Tilia cordata Mill.), hornbeam (Carpinus betulus L.), maples (Acer spp. L.), alder (Alnus glutinosa L.), willow (Salix caprea L.), and ash (Fraxinus excelsior L.). Dense herbaceous vegetation consisted mainly of Aegopodium podagraria L., Impatiens glandulifera (Royle), Lamium maculatum L., Phalaris arundinacea L., and Urtica dioica L. Humus-rich loamy soils with high moisture and a thick layer of leaf litter were noted at each site. Sampling sites were preselected to harbour rich populations of land snail species with different foraging and microhabitat preferences. The sampling campaign took place during a single day in the summer of 2019. With the assistance of four people for about half an hour, the dominant species of land snails were collected by hand, using soft forceps at each of the sites. We did not sample the entire land snail assemblage, however, based on our survey during sampling, the total number of land snail species at each site was similar, approximately 20 species. In total, 189 individuals including 17 land snail species were collected, and every individual was fixed and preserved in 99.8% ethanol separately, all of them were grown-up individuals. Only species with at least five collected individuals per site were included in the analysis, resulting in 60 individuals of seven species at site A, 69 individuals of nine
species at site B and 45 individuals of five species at site C (table 1).

Under a dissection microscope, snail soft tissues (foot muscle) were isolated from each individual to obtain stable isotope signatures of Nitrogen and Carbon. The shell and digestive system were removed as these could contain non-organic and undigested N and C sources, respectively. Nitrogen isotope ratio is used to indicate the trophic position of an organism in a food web due to the stepwise accumulation of $^{15}$N in the higher levels of food webs (Post, 2002; Pollierer et al., 2009). In contrast, carbon isotope ratio remains relatively the same through trophic levels. It may be used in determining the primary production source responsible for the energy flow in an ecosystem (e.g., plants with C$_3$ and C$_4$ photosynthetic pathways; Peterson & Fry, 1987; Ostrom et al., 1997). The samples of snail foot were cut into small pieces and dried at 55°C for 48 h. The samples were prepared with weighing accuracy of 0.01 mg to contain a range of 200–2000 µg C and 20–150 µg N content, and then sent to UC Davis Stable Isotope Facility for analytical services – dual $^{13}$C and $^{15}$N natural abundance analysis.

The obtained data file was extended by the published data of 60 individuals of six species (site D; table 1) adopted from Němec et al. (2021). The sampling site represented floodplain forest situated in the Odra River alluvium (49.72208N, 18.11128E), Czech Republic. We were able to include this data as completely the same method of sample collection and processing, data preparation and isotope measurements were used.

**Dataset compilation**

To calculate the average values of both C and N isotope signatures for each land snail species per site (supplementary table S1) and to create stable isotope biplots, we used the conventional $\delta$ (delta) notation of natural abundances of stable isotopes for a given material, defined as the parts per thousand (‰) deviation from standard material. The equation for $\delta^{13}$C or $\delta^{15}$N is equal to: $(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1) \times 1000$, where $R$ = $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N, respectively. The established standard for $\delta^{13}$C was Pee Dee Belemnite (PDB) and for $\delta^{15}$N atmospheric nitrogen. Stable isotope data analyses were performed using the packages Stable Isotope Bayesian Ellipses in R (siber v2.1.5; Jackson

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**FIGURE 1** Isotopic niches represented by Standard ellipse area corrected for small sample size (seac) of the land snail species collected in four study sites (A, B, C, D) at least in five individuals per site.
et al., 2011; Parnell & Jackson, 2017). In order to estimate isotopic niches of land snails based on their δ13C and δ15N signatures, we applied Bayesian approach, fitting a Bayesian multivariate normal distribution to each group in the dataset. Firstly, we calculated the small sample size corrected standard ellipse area (SEAC) to obtain trophic niche size of each group (table 1), i.e., individuals of a given species at the site. The SEAC incorporates the 40% densest data points within a dataset (Jackson et al., 2011). This approach has been developed to particularly account for comparison of species with small and variable sample sizes (Parnell et al.,

### Table 2

| Variable            | Min  | 1 Q  | Median | Mean  | 3 Q  | Max  | Transfor. |
|---------------------|------|------|--------|-------|------|------|-----------|
| **Dependent**       |      |      |        |       |      |      |           |
| SEAC                | 0.40 | 0.70 | 1.66   | 2.59  | 3.60 | 9.99 | Logarithmic |
| Overlap (%)         | 0.00 | 0.00 | 0.00   | 24.57 | 51.92| 100  | Square root |
| **Explanatory (numeric)** |      |      |        |       |      |      |           |
| No. individuals (for SEAC analysis) | 5    | 7    | 10     | 8.67  | 10   | 10   | None      |
| No. individuals (for Overlap analysis) | 10   | 15   | 17     | 16.98 | 20   | 20   | None      |
| Body size           | 87.0 | 283.5| 478.0  | 3490.1| 3137.0| 21701.0| Logarithmic |
| Difference in body size | 2    | 210  | 2645   | 5746  | 5938 | 21576| Logarithmic |
| **Explanatory (categorical)** |      |      |        |       |      |      |           |
| Site                | A, B, C, D |
| Lifestyle           | Epigean, Opportunistic, Arboreal |
| Difference in lifestyle | Similar, Overlapping, Different |

### Table 3

Results of generalised estimating equations (GEE) model (family: gaussian, link: identity) for land snail SEAC values as the response variable. P(>|Chi|) = p-value of the Chi-square statistic. Note that lifestyle and individual body size were highly significant.

| Variable               | Df | X²  | P(>|Chi|) | Significance |
|------------------------|----|-----|----------|--------------|
| No. of collected individuals | 1  | 0.1 | 0.74     | n.s.         |
| Lifestyle              | 2  | 225.8 | <0.001   | ***          |
| Body size              | 1  | 21.3 | <0.001   | ***          |
Secondly, percentage of overlap in seac for pairwise species combinations was calculated for each of the sites. We used function overlap.xypolygon from the ‘spatstat’ package family (version 2.3–2; Baddeley et al., 2015), where the polygons were represented by the seac of the given species, based on ellipses presented in the fig. 1.

Land snail lifestyle was classified according to microhabitat preferences based on literature data and also our evidence observed during the field sampling as (i) epigean, species dwelling in leaf litter and/or upper soil layer; (ii) opportunistic, species that commonly behave as epigean, but also often climb up vegetation, mostly herbaceous; (iii) arboreal, species that are mostly or exclusively associated with trees or deadwood, avoiding leaf litter. Additionally, the difference in lifestyle was evaluated as (i) similar, the compared species are both classified in the same lifestyle type; (ii) overlapping, one of the compared species is classified as either epigean or arboreal and the other one as opportunistic and (iii) different, i.e., one of the compared species is classified as epigean and the other one as arboreal. The body size of the snail species was defined as the volume of the shell, calculated according to the formula given in McClain & Nekola (2008) as the volume of the cone resting on the top of the cylinder determined by visual evaluation of photographs of snail shells. The difference in body size was calculated as the difference between the individual body sizes of the two species.

Thus, seac and percentage of overlap in seac represented the two dependent variables. The seac was tested against explanatory variables, including number of collected individuals, lifestyle, and body size for each land snail species (table 1). The overlap in seac was tested against explanatory variables including site, number of collected individuals combine for the two species, difference in their lifestyle, and body size. Both dependent and explanatory variables and their range are summarised in table 2.

**Statistical analysis**

To analyse variation in species seac in relation to their lifestyle and body sizes, generalised estimating equations (gee) with Gaussian distribution was used (gee-g). The seac and body size of each species were transformed prior the analysis using natural logarithm as the data were not normally distributed (table 2). gee is an extension of the generalised linear models for situations when measurements of the response variable are not independent. In our study there were multiple species collected from the same site, which gave rise to a correlated response per site, so we assumed exchangeable correlation structure in the residuals in order to correct for standard errors of parameter estimates that were too small. As seac value can be expected to increase with increasing sample size, we included the number of analysed individuals per species into the model as the first predictor, to control for variable sample size. gee-g were fitted using a function from the ‘geepack’ package (version 1.3–2; Højsgaard et al., 2006). The significance of all predictors was tested by the model, using Wald test.

Variation in percentages of overlapping seac for pairwise species combinations was analysed by generalised linear regression model (glm) using quasi-Poisson distribution with log link function (glm-qp) to correct for an overdispersion. We tested whether the overlap in seac is different between study assemblages and types of lifestyle and is changing with body size difference. As the number of analysed individuals varied, sums of individuals in the compared pair of species were the first predictor added into the model. The significance of all predictors was tested by the model, using Chi-square statistic. The size of the overlapping area was transformed using
square root transformation to normalise its distribution, the difference in body size was transformed using natural logarithm (table 2).

All analyses and graphics were performed in R program, version 4.0.2 (https://www.r-project.org/).

**Table 4** Results of generalised linear regression model (GLM; family: quasipoisson, link: log) for the size of the overlapping SEAC for each land snail pairwise combination as the response variable.

$P(>|\text{Chi}|)$ = p-value of the Chi-square statistic. Note that, number of collected individuals and difference in lifestyle were highly significant.

| Variable                      | Df | Deviance | Resid. Df | Resid. Dev | $P(>|\text{Chi}|)$ | Significance |
|-------------------------------|----|----------|-----------|------------|---------------------|--------------|
| NULL                          |    | 81       | 81        | 445.94     |                     |              |
| No. of collected individuals  | 1  | 85.186   | 80        | 360.75     | $<0.001$            | ***          |
| Site                          | 3  | 13.215   | 77        | 347.54     | 0.32                | n.s.         |
| Difference in lifestyle       | 2  | 49.478   | 75        | 298.06     | 0.001               | **           |
| Difference in body size       | 1  | 9.607    | 74        | 288.45     | 0.11                | n.s.         |
Results

In total, we analysed 234 individuals of 16 land snail species (table 1). *Zonitoides nitidus* was the smallest analysed species (shell volume of 87 mm$^3$), while *Helix pomatia* the largest (21,701 mm$^3$). Four species were assigned as epigean, nine opportunistic and three arboreal (see table 1). Out of 27 calculated seac, the lowest value was recorded for *Aegopinella ressmanni* at site B (0.40) and the highest for *Oxyloma elegans* at site D (9.99), with the median of 1.66 (table 2). While there were overlaps of seac among the most species in the analysed assemblages, some species express rather exclusive isotopic signature (i.e., *Macrogastra ventricosa* at site A, *Cochlodina laminata* at site B, *Cepaea hortensis* at site C and *Z. nitidus* at site D, fig. 1). Because of these species, 44 out of all 82 pairwise comparisons resulted in a zero overlap. In contrast, a complete overlap was recorded in four cases where the ellipse of one species was nested within an ellipse of another species.

**seac analysis**

We found that the number of analysed individuals per species was not significantly impacting their seac values (GEE, $p = 0.74$). In contrast, both lifestyle (GEE, $p < 0.001$) and body size (GEE, $p < 0.001$) were found to be significant (table 3). Epigean species had significantly smaller seac than arboreal species, while opportunistic species were intermediate in their seac, with not significant difference from any of the others (fig. 2a). Smaller species not only had significantly larger seac than the larger species but showed also higher variability (fig. 2b).

**Analysis of overlap in seac**

The percentages of overlapping seac areas for pairwise species combinations were found to be significantly impacted by the number of collected individuals (GLM-gp, $p < 0.001$) and the difference in species’ lifestyle (GLM-gp, $p = 0.001$; table 4). In contrast, no significant effect was detected for body size difference (GLM-gp, $p = 0.11$) and site (GLM-gp, $p = 0.32$, table 4), although site B slightly differed from the other sites (fig. 2c). Species with different lifestyle did not overlap in their isotopic niches, but one pair of species with a small overlap. By contrast, species with similar lifestyle were highly variable in their overlapping seac, resulting in significantly higher percentage of overlap that those of the remaining categories (fig. 2d).

Discussion

Stable isotope analysis can be used in a variety of ways to study foraging ecology and trophic relationships among organisms, because it provides a temporally integrated view of matter fluxes. In the present study, we found a high degree of overlap among isotopic niches of land snail species. This pattern has been documented previously and suggests that there is little or no trophic niche compartmentalisation between co-occurring land snail species (Schmidt et al., 2004; Bonkowski & Kappes, 2017; Němec et al., 2021). Consequently, the extent of food competition is generally considered negligible, as a virtually unlimited amount of food resources for snails can usually be expected. Furthermore, land snails are considered true opportunists in their feeding ecology, seeking out a large number of potential food sources along the way (Speiser, 2001).

Nevertheless, we observed a significantly different position in the isotopic niche space for arboreal snails compared to the others, mainly because of the lower $\delta^{15}$N values. This resulted in non-overlapping seac ellipses between these groups, indicating differences in diet (Jackson et al., 2011). The arboreal snails also had the significantly highest trophic niche size (expressed by their seac). This result...
should be taken with caution because of the strong phylogenetic clustering, since two of the three arboreal species are clausilids. However, the third arboreal species (Ena montana) is phylogenetically distant and similar results on differences in trophic niche position for arboreal snails compared to ground-dwelling snails were also noted by Saeki et al. (2017). This is likely related to the fact that epiphytic lichens and mosses, i.e., food sources with different δ13C and δ15N signatures, are consumed more frequently than litter and live plant biomass. Given that trees and decaying deadwood are habitats of highly diverse lower plant flora and fungi (Crites & Dale, 1998; Vellak & Paal, 1999), we hypothesise that snails using this type of microhabitat may utilise a broader range of food resources. Such a distinct isotopic signatures lead to larger trophic niche size. In addition, coarse deadwood also provides a wide range of shelters (Kappes, 2005; Müller et al., 2005), which may reduce the need for mobility and contribute to greater diversity in the isotopic signatures of arboreal land snails. In contrast, epigean snails probably all feed on the same mixture of leaf litter and, in some cases, live plant biomass, resulting in a more homogeneous signatures across individuals and thus a smaller trophic niche size.

Our results also suggest a significant difference in niche size relative to body size. Because several traits correlate with body size, the mechanism causing this relationship is not clear. Species with larger body size are more mobile (e.g., Baur & Baur, 1988; Dahirel et al., 2015) and need to consume a proportionally greater amount of food resources during costly locomotion (Denny, 1980; Cook, 2001). Despite the presumably wide range of food sources resulting from opportunistic feeding, there is little variation among individuals. This may result in similar isotopic signatures among all individuals, and thus a smaller trophic niche size. In contrast, small body-sized species are thought to have limited mobility (Dahirel et al., 2015). Thus, individuals are thought to be more closely tied to a specific microhabitat, likely characterised by unique food resources. These factors may lead to distinct signatures among individuals and thus a larger trophic niche. It should be noted that in our study, large species were often epigean, whereas most small species were arboreal, so the effects of individual body size and lifestyle may partially overlap. However, because the effect of body size was tested for residual variation (i.e., when the effect of lifestyle is removed) and was still significant, it is clear that there is variation related solely to the effect of body size. A combination of low mobility and the presence of more diverse and spatially structured food sources makes the diet of individuals unique. Thus, we hypothesise that trophic niche size is closely related to lifestyle and body size/mobility of land snail species and is greater in arboreal, small body-sized species due to limited mobility.

Although there were systematic trends among species, we also observed variation in niche size between populations of several species. This was most pronounced for Macrogastra ventricosa at sites A and B. It seems that this could be related to habitat heterogeneity and food diversity. Site A is a scree forest, where a greater number of different tree and herb species were observed (Hájek et al., 2020) than at site B. This site was an alder forest in flat terrain with a more uniform tree and herb composition than at site A. Consistent with this, M. ventricosa exhibited a notably more uniform trophic niche at site B than at site A. While the effect of site on seac ellipse overlap was not significant, we observed some differences between them. The differences were most pronounced at site B, likely due to the higher proportion of arboreal species sampled at this site. This is also supported by the fact that the degree of ellipse overlaps generally increased with a higher proportion of epigean species. Moreover, the arboreal species at site B did not overlap with each
other; for example, no overlap was captured between *Cochlodina laminata* and other arboreal species. Here, the relative habitat uniformity at this site could lead to the observed differentiation in species trophic niche if species are spatially separated and therefore use different food sources. In contrast to the variation among species populations, the number of individuals collected had a significant effect on the percentage of overlap among species in an assemblage. In other words, the more individuals collected, the greater the likelihood that overlap between species will be recorded. As more individuals are sampled, the degree of trophic niche overlap increases until eventually all species within an assemblage overlap, likely with the exception of some epigean and arboreal species, which presumably have partially different diets as they have different microhabitat preferences. This fits with the general assumption that most land snail species are opportunists (Speiser, 2001).

In conclusion, using the isotopic niche approach, we have demonstrated that most land snail species within an assemblage share a common trophic niche as previously expected. Given the generalist feeding behaviour of most land snail species and the ample amount of available food sources, we hypothesise that this shared niche is not due to their feeding specialisation, but rather to their direct use of space in the microhabitat, i.e., the lifestyle. The size and position of the trophic niche is likely influenced by the use of different and unique food sources by individuals of smaller land snail species combined with their lower mobility. On the contrary, a different pattern is expected for large species with good mobility, as all individuals use the same broad mixture of food sources.

**Acknowledgments**

This study was supported by the Masaryk University Institutional Grant for Doctoral Students and primarily by the Czech Science Foundation (GA20-18827S). We also thank two anonymous reviewers for their valuable comments, and Veronika Horsáková, Jeffrey C. Nekola and Radovan Coufal for their help in collecting live snails in the field.

**Supplementary material**

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.21062770

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