

1 **Urban *Cepaea nemoralis* snails are less likely to have** 2 **nematodes trapped within their shells**

3 Maxime Dahirel*, Hannah Reyn , Katrien De Wolf, Dries Bonte

4 Ghent University, Department of Biology, B-9000 Gent

5 ORCID:

6 MD: 0000-0001-8077-7765

7 KDW: 0000-0002-9255-913X

8 DB: 0000-0002-3320-7505

9 *corresponding author: maxime.dahirel@yahoo.fr

10 **Abstract**

11 Urbanization is a major human-induced environmental change which can impact not only
12 individual species, but also the way these species interact with each other. As a group, terrestrial
13 molluscs interact frequently with a wide diversity of parasites, yet the way these interactions vary
14 across space and in response to environmental pressures is poorly documented. In this study we
15 leveraged a recently discovered defence mechanism, by which snails trap parasitic nematodes in
16 their shells, to explore how snail-nematodes interactions may vary in response to city life. We
17 examined shells from the generalist snail *Cepaea nemoralis* sampled in three urban areas in
18 Belgium for trapped nematodes, and attempted to link this to urbanization and shell phenotypic
19 traits. We found that even a small degree of urbanization led to large decreases in the rates of
20 shell encapsulation, and that larger snails were more likely to contain trapped nematodes.
21 However, we found no evidence that shell colour, which had been previously linked to immune
22 function, was correlated to encapsulation rates. We discuss how between-population variation in
23 encapsulation rates can result from urbanization-induced changes on the nematodes side, the
24 snail side, or both, and suggest potential tests for future studies aiming to disentangle these
25 mechanisms.

26 **Key words:** Biotic interactions, Gastropoda, immunity, parasites.

27

28 Introduction

29 Urbanization is a major and all-encompassing human-induced environmental change, leading to
30 changes in land use, local climate, soil imperviousness, light and chemical pollution... (Parris,
31 2016). The (often negative) impacts of these multivariate changes on biodiversity are increasingly
32 well-documented: many species decline in cities, while some become successful “urban
33 adapters”, leading to major restructuring of biological communities along urbanization gradients
34 (e.g. McKinney, 2008; Piano et al., 2020; Fenoglio et al., 2020; Liang et al., 2023). In parallel,
35 urbanization can also cause within-species phenotypic and genetic changes (Alberti et al., 2017;
36 Szulkin et al., 2020; Diamond & Martin, 2021). Urbanization may also have second-order impacts
37 by reshaping ecological interactions, if tightly connected species respond to environmental
38 change in different ways (Theodorou, 2022). Such urbanization-induced changes in ecological
39 interactions, in both positive and negative directions, have been recorded for plant-pollinator
40 interactions (Liang et al., 2023), plant-herbivore and prey-predator interactions (Eötvös et al.,
41 2018; Valdés-Correcher et al., 2022; Gámez et al., 2022; Korányi et al., 2022), as well as host-
42 parasite interactions (Murray et al., 2019; Korányi et al., 2022).

43 Terrestrial molluscs (snails and slugs) are potentially valuable models in urban ecology and
44 evolution, in part because of their limited movement abilities, which means they often cannot
45 move to escape environmental changes. Like in many other taxa, urbanization can reshape
46 molluscan communities (Lososová et al., 2011; Horsák et al., 2013; Barbato et al., 2017; Hodges
47 & McKinney, 2018), and drive evolutionary responses in urban populations (Kerstes et al., 2019).
48 Interestingly, in a comparative cross-taxon study of urbanization impacts, snail species richness
49 were less negatively affected, compared to other more mobile groups (Piano et al., 2020). Land
50 molluscs are hosts to a diverse array of metazoan parasites, including nematodes, flies, mites or
51 trematodes (Barker, 2004; Segade et al., 2013; Žbikowska et al., 2020). How urbanization
52 reshapes these interactions remains understudied, despite some of these parasites being of
53 increasing veterinary interest (Aziz et al., 2016; Giannelli et al., 2016).

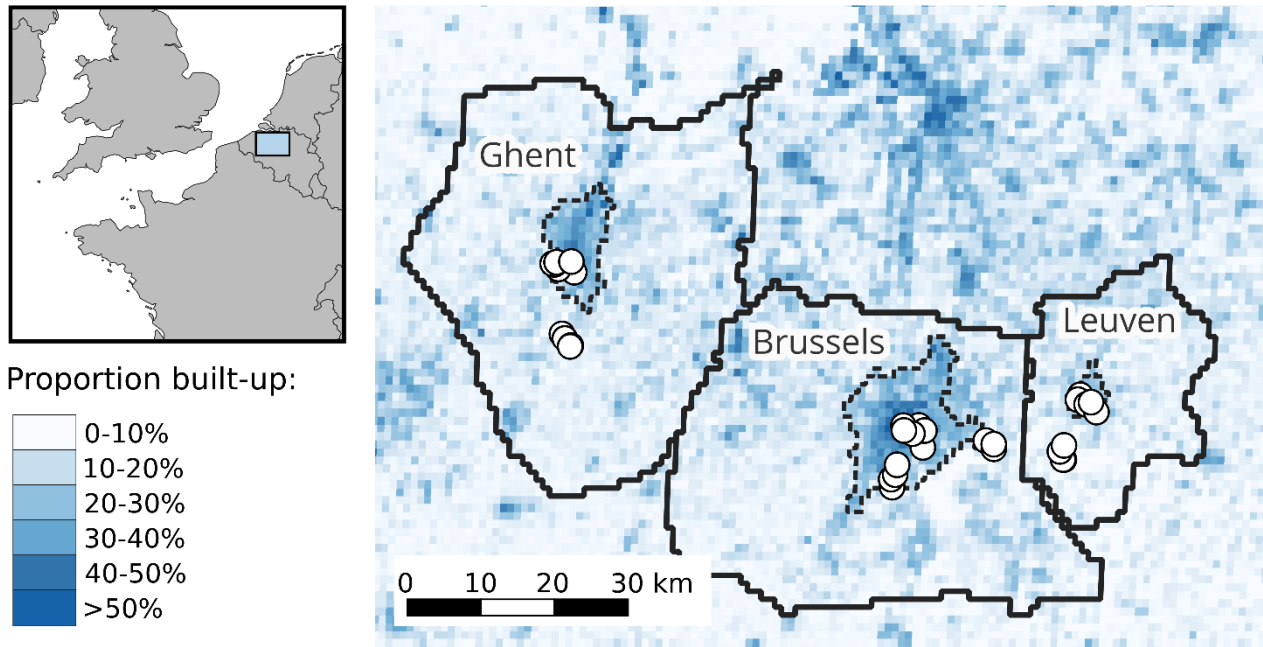
54 Snails and slugs can defend themselves against metazoan parasites through a variety of
55 behavioural (Wilson et al., 1999; Wynne et al., 2016; Rae, 2023) or immune responses (Furuta &
56 Yamaguchi, 2001; Scheil et al., 2014; Coaglio et al., 2018). Among the latter, it has been discovered
57 that land molluscs can use their shells to trap parasitic nematodes, killing them and fusing them
58 to the inner shell surface (Rae et al., 2008; Williams & Rae, 2015; Rae, 2017). This ability seems
59 phylogenetically widespread, even present in slugs with vestigial shells (Rae et al., 2008; Rae,
60 2017), and could therefore provide a relatively easy to access record of ecological interactions.
61 Following anecdotal records of mites and trematodes encapsulated in shells, it has further been
62 suggested that this shell encapsulation might extend to other metazoan parasites (Dahirel et al.,
63 2022; Gérard et al., 2023). However, given how rare these non-nematode records are, they may
64 be merely by-products of a defence mechanism targeted towards nematodes, rather than
65 evidence of a more generalized defence response (Gérard et al., 2023). The few snail species in
66 which this phenomenon has been studied across multiple populations show that the prevalence
67 of individuals trapping nematodes can vary widely between sites (Rae, 2017; Rae, 2018;
68 Cowlshaw et al., 2019), but there has been no attempt, to our knowledge, to assess whether this
69 variation could be non-random with respect to environmental context.

70 To that end, we combine here publicly available and standardized urbanization metrics with
71 observations of field-collected snails across three cities in Belgium, using the grove snail *Cepaea*
72 *nemoralis* (Gastropoda, family Helicidae) as a model. Like other helicids, *C. nemoralis* can
73 encapsulate and trap parasitic nematodes in its shell (Williams & Rae, 2016; Rae, 2017; Dahirel et
74 al., 2022; Gérard et al., 2023). This snail is also common both outside and within cities (Kerstes et
75 al., 2019), and therefore a very suitable model to study variation in encapsulation rates, whether
76 it is due to urbanization or to spatial (between-cities) differences. Furthermore, the shell colour
77 variation that made *Cepaea* species iconic models in evolutionary biology (Jones et al., 1977;
78 Özgo, 2009) may also influence their immune response, with some evidence that darker morphs
79 mount better defences against nematodes (Dahirel et al., 2022; but see Scheil et al., 2014). On
80 the other hand, this morph variation in resistance might not translate to shell encapsulation
81 (Williams & Rae, 2016; Dahirel et al., 2022). However, existing comparisons were either limited
82 to one type of colour variation (banding pattern only, Dahirel et al., 2022), or analysed
83 experimental infections by one model nematode (Williams & Rae, 2016); we here test whether
84 this remains true when analysing naturally occurring snail-nematode interactions and accounting
85 for more dimensions of shell colour variation.

86 **Methods**

87 **Site selection and sampling**

88 We searched for *Cepaea nemoralis* snails from early October to mid-November 2022 in and
89 around the urban areas of Brussels, Ghent and Leuven in Belgium (**Fig. 1**). Potential sites were
90 selected based on pre-existing online crowdsourced records (iNaturalist contributors &
91 iNaturalist, 2024) combined with personal observations and virtual fieldwork using Google
92 StreetView to identify suitable habitats (based on Falkner et al., 2001). We visited 36 sites chosen
93 to be roughly balanced between the three cities (including their surrounding areas; Brussels: 13
94 sites, Ghent: 13 sites, Leuven: 10 sites). In each site, we sampled living snails by hand during visual
95 search, in a radius of up to 50 m around a designated site centroid (though search was *de facto*
96 mostly concentrated within a 20 m radius). Individuals were mainly searched in known favourable
97 micro-habitats, i.e. on tall herbs and shrubs, under piled wood and cardboard or loose rocks, or
98 on fences, walls, and tree trunks (Falkner et al., 2001). Field identification of *Cepaea nemoralis*
99 snails is easy based on shell shape, size and colour (Cameron, 2008). We only collected adults,
100 which can easily be separated from subadults by the presence of a reflected shell lip marking the
101 end of shell growth (Cameron, 2008). Each site was visited by 1 to 3 people (mean: 2.03) for a
102 duration of 5 to 30 person-minutes (mean: 15). We collected a total of 298 snails from 28 of the
103 36 sites visited (Brussels: 9 sites, Ghent: 10 sites, Leuven: 9 sites). However, 2 shells were lost
104 before examination for parasites due to handling errors, and another shell was accidentally
105 broken for parasite examination before photographs or size measurements could be done; this
106 led to a final complete dataset of 295 snails in 28 sites. For each of these 28 sites, the nearest
107 neighbouring site with snails found was between 153 and 1516 m away (mean: 768 m), which is
108 in any case farther than the maximal dispersal distances (Kramarenko, 2014), indicating that even
109 nearby sites could be considered separate populations.



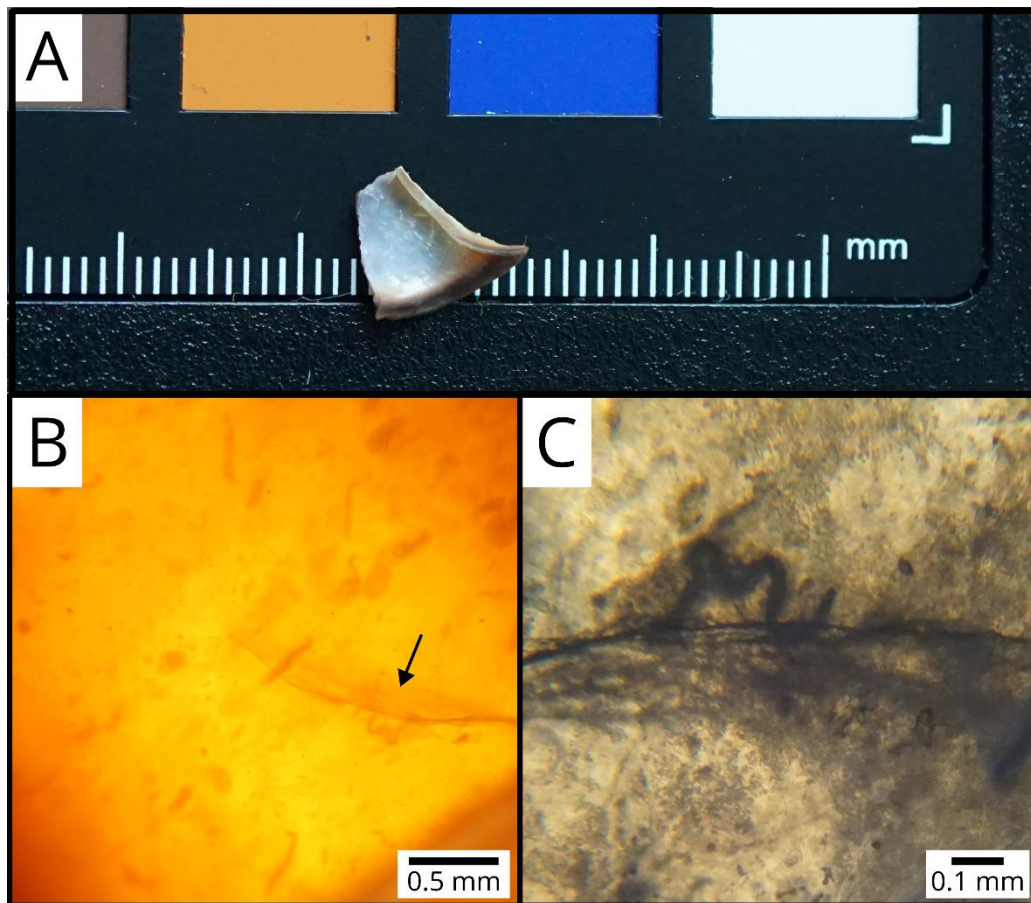
110
 111 **Figure 1.** Location of study sites within western Europe and central Belgium. The Functional Urban Areas
 112 (roughly corresponding to commuter zones, Schiavina et al., 2019; Moreno-Monroy et al., 2021) that were
 113 used to link each site to a city are also displayed as solid black lines, while the corresponding core urban
 114 areas (Urban Centres *sensu* Eurostat (European Commission), 2021; Schiavina, Melchiorri, et al., 2023) are
 115 displayed with dashed lines.

116 **Urbanization metrics**

117 It is well-known that urban environmental changes are complex and multivariate (e.g. Parris,
 118 2016); however, given our relatively low number of sites, and the risk of collinearity between
 119 urban metrics, we decided to use simple overarching metrics focused on building presence and
 120 human population density. We assessed urbanization at each site using raster layers from the
 121 Global Human Settlement Layer project for the year 2020 (<https://ghsl.jrc.ec.europa.eu/>, Joint
 122 Research Centre (European Commission), 2023). We first used built-up surface (GHS-BUILT-S) and
 123 population density (GHS-POP) at 100 m and 1000 m resolutions (Pesaresi & Politis, 2023;
 124 Schiavina, Freire, et al., 2023). The former spatial scale matches the scale of maximal dispersal
 125 movements over timespans of up to a couple years in helicid snails, while the latter is closer to
 126 the scale of longer term (over several decades) population spread (Kramarenko, 2014). As an
 127 additional categorical metric, we also used the Degree of Urbanization as recorded in the
 128 Settlement Model layer (GHS-SMOD, available only at 1000 m resolution, Eurostat (European
 129 Commission), 2021; Schiavina, Melchiorri, et al., 2023). At the highest level of classification, the
 130 standardized Degree of Urbanization methodology mainly uses population density and contiguity
 131 rules to classify grid cells as either part of a continuous high-density Urban Centre, as low-density
 132 rural cells or as intermediate peri-urban/suburban cells. For each site and urbanization metric,
 133 we recorded the value of the corresponding grid cell. Interestingly, Degree of Urbanization
 134 classes, primarily based on population density, divide our sites in almost the same non-linear way
 135 as another, independent, three-level classification based on built-up surfaces used in previous
 136 urban ecology studies in the study region (e.g. Piano et al., 2020) (**Supplementary Material S1**).

137 **Snail shell analysis**

138 Snail size was measured using a caliper as the shell greatest diameter (to the nearest 0.1 mm).
139 Snail shell colour morphs were scored following e.g. Cain (1988) for background colour (from
140 lighter to darker: yellow, pink or brown), number of dark bands (0 to 5 bands) and on the presence
141 or absence of band fusions (which increase the proportion of the shell covered by dark bands).
142 Snails were killed by first inducing dormancy at 6°C, then by freezing at -20°C. We removed bodies
143 from shells with forceps and lightly cleaned shells with water (bodies were stored in ethanol for
144 separately planned studies). We then broke each shell into fragments using forceps, examined
145 fragments under a binocular microscope, and recorded all animals found encapsulated within the
146 shell as in e.g. Gérard et al. (2023). A total of 606 nematodes were found in 104 shells (**Fig. 2**); we
147 found no mites, trematodes or other parasites in any of the shells. Shells with nematodes
148 contained 5.83 nematodes on average (SD: 9.95, range: 1-58). As this method is destructive, we
149 took standardised photographs of the shells beforehand (dorsal and apertural views following
150 Callomon, 2019) for archival and potential future studies.



151
152 **Figure 2.** Fragment of a *Cepaea nemoralis* shell (A) containing encapsulated nematodes (B, C). The arrow
153 in (B) points to the nematode shown in (C).

154

155 Statistical analysis

156 All analyses were done in R version 4.3.2 (R Core Team, 2023), with the help of the *tidyverse*
157 (Wickham et al., 2019) and *sf* (Pebesma, 2018) packages for data processing, as well as additional
158 packages detailed below for model fitting and exploration.

159 We analysed the probability a shell contained nematodes as a binary yes/no response at the
160 individual level, using Generalized Linear Mixed Models (GLMMs) (binomial family, logit link). We
161 ran six models; the first five all included shell size, shell morph traits (background colour, band
162 number and fusion), urbanization and city identity (Brussels, Ghent or Leuven) as fixed effects,
163 only differing by which urbanization metric they used (among the five described above in
164 **Urbanization metrics**). Given our sample size, we did not include interactions between our
165 explanatory variables, especially as we had no *a priori* hypotheses regarding these (but see
166 **Discussion**). Numeric predictors were centred and scaled to unit 1 SD. Sampling site was included
167 as a random intercept. The sixth model was a “null” model, identical to the other ones except
168 that it did not include an urbanization metric. We ran our models using the *glmmTMB* package
169 (Brooks et al., 2017), and then used AICc to compare them. As one model largely outperformed
170 the others (see **Results**), we did all further analyses on that best model.

171 We checked for residual spatial autocorrelation using a spline correlogram (*ncf* package,
172 Bjornstad, 2022), and found no evidence of spatial structure in the best model. We then used the
173 *car* (Fox & Weisberg, 2019) and *emmeans* (Lenth, 2023) packages to test for overall effects of our
174 variables in the best model and to run (Tukey-corrected) pairwise comparisons, respectively.
175 Finally, we estimated the marginal and conditional R^2 (Nakagawa & Schielzeth, 2013) as measures
176 of the proportion of variation explained by fixed effects (R_m^2) and both fixed and random effects
177 (R_c^2) respectively (using the delta method, Nakagawa et al., 2017).

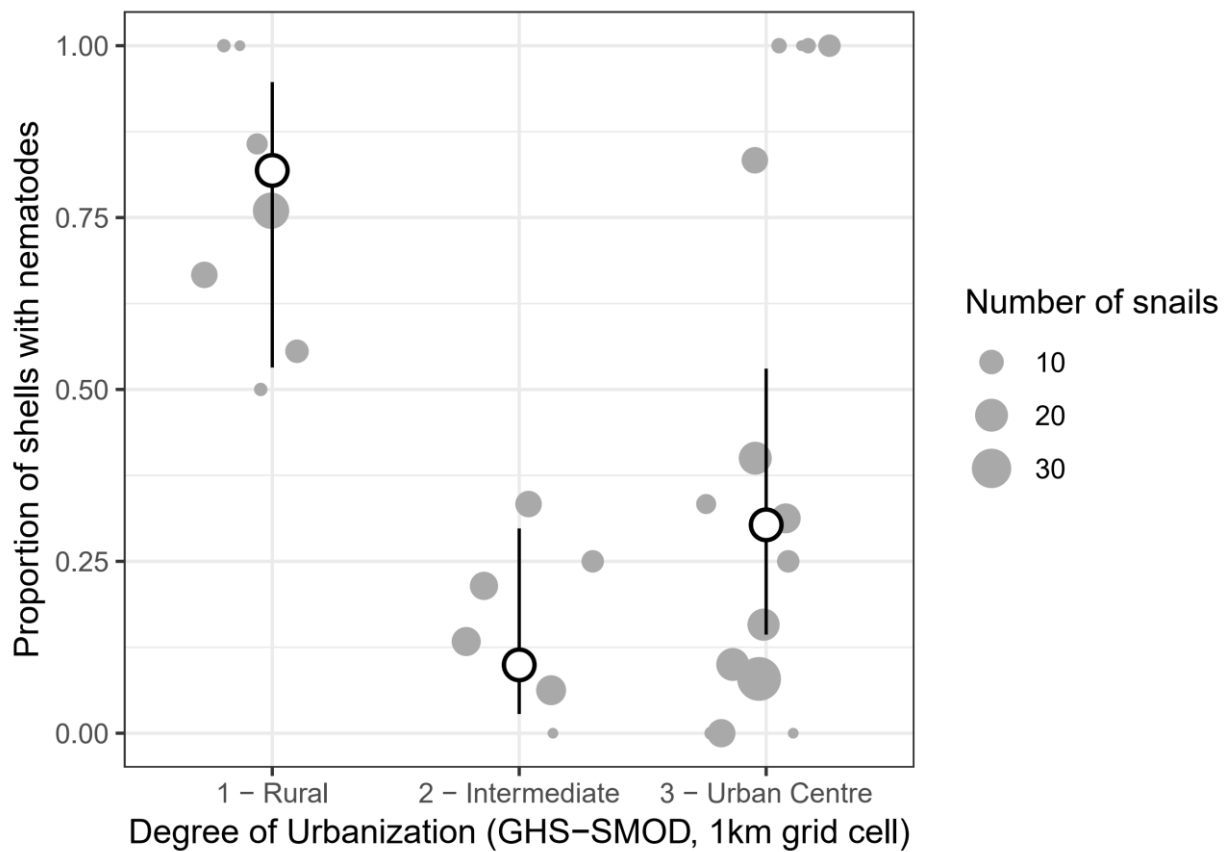
178 Results

179 The model using the categorical Degree of Urbanization (GHS-SMOD) as an urbanization metric
180 outperformed all other models based on AICc (**Table 1**). Fixed effects and random effects
181 explained similar amounts of variance ($R_m^2 = 0.19$; $R_c^2 = 0.38$). The probability that a shell had
182 trapped nematodes was dependent on urbanization level ($\chi^2 = 15.97$, $df = 2$, $p = 3.40 \times 10^{-4}$)
183 but did not vary significantly between cities ($\chi^2 = 3.89$, $df = 2$, $p = 0.14$). Snails from rural sites
184 were more likely to contain nematodes than snails from intermediate and Urban Centre
185 populations (**Fig. 3**; rural - intermediate difference on the logit scale \pm SE: 3.71 ± 0.95 ; rural -
186 Urban Centre difference: 2.34 ± 0.77). Larger shells were more likely to contain nematodes ($\chi^2 =$
187 4.17 , $df = 1$, $p = 0.04$; standardised coefficient $\beta = 0.35 \pm 0.17$). There was no clear evidence
188 that any of the shell colour traits affected encapsulation rates (background colour: $\chi^2 = 2.17$,
189 $df = 2$, $p = 0.34$; band number: $\chi^2 = 1.90$, $df = 1$, $p = 0.17$; fusion: $\chi^2 = 0.17$, $df = 1$, $p =$
190 0.68).

191

192 **Table 1.** Model selection table for the effect of urbanization on shell encapsulation rates. All models
 193 otherwise include effects of city identity, shell size and shell morph (background colour, number of bands
 194 and band fusion).

Urbanization variable in model	df	log-likelihood	AICc	Δ	AICc weight
Degree of Urbanization categories (SMOD, 1000 m resolution grid)	11	-149.5	322.0	0.00	0.95
None ("null" model)	9	-155.9	330.4	8.43	0.01
Population density (1000 m resolution grid)	10	-155.2	331.1	9.11	0.01
Built-up surface (1000 m resolution grid)	10	-155.4	331.5	9.49	0.01
Population density (100 m resolution grid)	10	-155.4	331.6	9.61	0.01
Built-up surface (100 m resolution grid)	10	-155.6	331.9	9.91	0.01



195 **Figure 3.** Effect of the Degree of Urbanization in 1000 m grid cells on the probability a snail shell contained
 196 encapsulated nematodes. Grey dots are observed proportions per population, with the size of the dot
 197 proportional to the number of snails; white dots (and error bars) are estimated marginal means from the
 198 best model (and their 95% confidence intervals), with the effects of the other predictors averaged out.
 199

200 Discussion

201 We found that the prevalence of *Cepaea nemoralis* snails encapsulating nematodes in their shell
202 as a defence mechanism were partly driven by environmental conditions, with lower trapping
203 rates in more urban sites (**Fig. 3**). This effect was better explained by a categorical classification
204 of the Degree of Urbanization, rather than by linear effects of continuous urbanization variables.
205 This indicates that the response to urbanization is non-linear, as the increases in population
206 density/built-up rates needed to go from a rural to an intermediate area are much smaller than
207 those needed to go from intermediate to Urban Centre, and most of the variation in density/built-
208 up is within Urban Centres rather than between categories (**Supplementary Material S1**).

209 A difficulty for interpreting our results is that nematodes trapped in shells accumulate with time
210 (Williams & Rae, 2015; Rae, 2017), meaning that as they may have endured more infections, older
211 snails may be more likely to have them. If the urban heat island influences snail survival rates
212 (Wolda, 1967, Manoli et al., 2019), then our urban-rural differences in nematodes trapped might
213 merely reflect differences in average snail age/survival. Age estimation in terrestrial snails is
214 challenging (Pollard et al., 1977; Williamson, 1979), and any age proxy is likely to be influenced
215 by local conditions, making it useless to compare age between populations without thorough
216 calibration studies. However, while there is substantial population variation, the number of
217 nematodes found in infected shells does not decrease in more urbanized sites (**Supplementary**
218 **Material S2**), contrary to what we would expect if variation in shell encapsulation was primarily
219 explained by variation in time available to accumulate nematodes.

220 If we assume that our results reflect differences in snail-nematodes interactions between urban
221 and non-urban areas, several mutually non-exclusive mechanisms may explain why urban *Cepaea*
222 *nemoralis* shells are less likely to trap nematodes. Each of these mechanisms directly suggests
223 potential tests for future studies:

- 224 • First, snail parasitic nematodes infecting *C. nemoralis* may be less abundant in cities. Many
225 nematodes known to infect land snails have at least one free-living life stage in the soil,
226 and some are facultative parasites (Morand et al., 2004; Pieterse et al., 2017). Increasingly
227 impervious substrates in cities (Parris, 2016) may deprive these of habitat critical for their
228 life cycle. Where habitat is available, soil nematode communities are profoundly altered
229 by urbanization, like other taxa (Li et al., 2022; Gong et al., 2024). However, this does not
230 lead to overarching declines in nematode abundance; rather, some trophic groups decline
231 while others thrive (Li et al., 2022; Gong et al., 2024). Unfortunately, detailed information
232 on nematodes parasitizing animals is typically lacking from these analyses; soil sampling
233 specifically targeting parasitic nematodes (Jaffuel et al., 2019) would be here particularly
234 useful. The few studies available are mixed on the effects of urbanization on the infection
235 of land molluscs by parasitic nematodes. In Wales, urban and suburban slugs are more,
236 not less, likely to be infected by *Angiostrongylus vasorum* compared to rural ones (Aziz et
237 al., 2016). By contrast, data from Andrus et al. (2022) spanning urban and non-urban sites
238 suggest that the prevalence of nematode infection may be slightly lower in urban
239 molluscs, although they did not themselves analyze the effect of urbanization. Both

240 studies however analyzed nematode prevalence in molluscs, not their
241 abundance/availability in the urban environment.

242 • Second, individual differences in behaviour, especially space-related behaviour, may lead
243 to differences in the risk of encountering and then being infected by parasites (Barber &
244 Dingemans, 2010). Habitat loss and fragmentation associated with urbanization are
245 expected to exert strong selection pressures on movement and space use (Cote et al.,
246 2017). If this results in lower movement in urban snail populations, this might then reduce
247 their encounter rates with parasites. In the snail *Cornu aspersum*, urbanization does not
248 lead to reduced habitat boundary-crossing behaviour (Dahirel et al., 2016), although that
249 is only one component of mobility. Urbanization-induced increases in temperature may
250 also alter the frequency at which snails hide into shelters or climb above the substrate
251 (Rosin et al., 2018), and potentially again the risk of encountering parasites. The picture is
252 complicated by behaviour-parasite feedbacks, where while host behaviour shapes
253 infection risk, infection can then alter host behaviour in turn (Ezenwa et al., 2016). In
254 *Cepaea nemoralis*, nematode infection itself might lead to reduced movement propensity,
255 but only in some morphs (Dahirel et al., 2022). More studies of movement behaviour
256 across urbanization gradients are here needed.

257 • Third, shell encapsulation rates are not direct records of snail-nematode interactions, but
258 rather informative on the host's ability to mount a defence in such interactions. This
259 defence is not always effective, as field-caught snails sometimes show active infections
260 but zero shell-trapped nematodes (see e.g. data in Dahirel et al., 2022). If immune
261 response declines with urbanization, then this alone could explain our results even in the
262 absence of changes in nematode communities. In vertebrates, urban living can lead to
263 both depressed or stimulated immune function, depending on taxon and context,
264 especially food availability (Murray et al., 2019; Minias, 2023). In terrestrial molluscs,
265 chemical pollutants seem to negatively impact many, but not all, physiological
266 components of immune defence (Radwan et al., 2020). The exact physiological pathways
267 involved in shell encapsulation in land molluscs remain however unstudied, to the best of
268 our knowledge.

269 Interestingly, nematode encapsulation prevalence was seemingly more variable between Urban
270 Centre populations than between populations in the other urban categories, with a few sites
271 having observed prevalences largely above the predicted mean (Fig. 3). While this may
272 merely simply be due to some sampling variability as these populations having low have very small
273 sample sizes, this suggests that there may could be non-random within-city variability in snail-
274 nematode interactions. As a first post-hoc exploration, we have re-run the models with
275 continuous urbanization variables as predictors, using only the Urban Centre subset of sites (see
276 Data and code availability). After accounting for phenotype and city of origin, we found no
277 indication that are not explained by built-up levels or population density. Cities are indeed levels
278 influenced prevalence within the Urban Centre category. Nonetheless, cities remain highly
279 heterogeneous environments, and even beyond built-up and population density; for instance,
280 within-city variation in vegetation, mediated in part by neighborhood-level socio-economic
281 differences, may shape biodiversity, including species interactions (e.g. Martin et al., 2024). Our

282 ~~ability~~ While we are not able to ~~detect within-city patterns is here~~ identify the causes of this
283 ~~heterogeneity in our current dataset, as we are~~ hampered by our small number of sites per Urban
284 Centre; future studies ~~focused on~~ designed to target this within-city heterogeneity may uncover
285 more on the fine-scale drivers of snail responses to parasites.

286 On the individual phenotype side, larger shells were more likely to contain trapped nematodes. If
287 shell size also varied in response to urbanization, then this could open an indirect pathway linking
288 urbanization to encapsulation mediated by snail size, potentially accentuating or dampening the
289 direct effect we describe above. However, we found no clear effect of urbanization on *C.*
290 *nemoralis* shell size (**Supplementary Material S3**). In addition and as a post-hoc exploration, we
291 re-ran our model set adding size × urbanization interactions, and found no significant interaction,
292 and no evidence that the urbanization effect changed in response (**Supplementary Material S4**).
293 The relationship between size and nematode encapsulation could be the result of survivor bias
294 alone, if larger snails are more likely to survive infection. However, and although we cannot
295 exclude that other nematodes have larger effects, experimental nematode infections by
296 *Phasmarhabditis* are almost never lethal in adult *Cepaea nemoralis*, contrary to other snail
297 species (Wilson et al., 2000; Williams & Rae, 2016). Other potential explanations for this result
298 can be sorted along three non-exclusive lines, similar to the mechanisms suggested above to
299 explain the effect of urbanization:

- 300 • Larger snails might harbour larger parasite infections (e.g. Daniels et al., 2013), which
301 would increase the likelihood that some nematodes are trapped. However, there is no link
302 between nematode abundance in active infections and snail size in *C. nemoralis* (Dahirel
303 et al., 2022), and no clear effect of shell size on the number of nematodes trapped in the
304 present study (**Supplementary Material S2**).
- 305 • If large and small snails differ in their space use, they might also differ in their parasite
306 exposure risk. Evidence for a link between shell size and space use is mixed in *Cepaea*
307 *nemoralis*, and this may depend on the scale of the movements in question (short-term
308 routine vs. dispersal movements; Oosterhoff, 1977; Dahirel et al., 2022).
- 309 • Finally, small and large snails may differ in their immune defence abilities. Comparative
310 studies suggest that large and small snail species and subspecies differ in their immune
311 strategies at the physiological level (Russo & Madec, 2011, 2013). However, the range of
312 body size and life history variation is much larger in these scenarios than among adults of
313 *C. nemoralis*, limiting the transferability of these results. More physiological studies
314 focused on within-, rather than among-species variation may help understand better this
315 link between body size and encapsulation rates.

316 In contrast to shell size, we found no relationship between any of the shell colour traits and
317 nematode trapping rate. This confirms experimental results from Williams & Rae (2016) using
318 infections by *Phasmarhabditis hermaphrodita*. However, colour morphs do differ in active
319 infection rates or other aspects of immune response in *C. nemoralis* (Dahirel et al., 2022) and
320 other polymorphic snails (Scheil et al., 2013, 2014). This discrepancy may indicate that shell

321 encapsulation is driven by different physiological pathways than other components of snail
322 immune defence.

323 Beyond the effects of phenotype or environment, whether and how the prevalence of nematodes
324 trapped in shells is correlated with rates of active parasite infections remains an open and
325 complex question (which we could not tackle here as snail bodies were reserved for other
326 investigations). If variation in snail-nematode interactions is driven by e.g. variation in nematode
327 density in the environment, we may expect a positive correlation, as higher nematode densities
328 should drive up rates of both shell encapsulation (Rae, 2018) and active infection (although if
329 encapsulation is highly effective, it may end up suppressing dose-dependent effects on active
330 infection, Williams & Rae, 2015). On the other hand, if variation is mostly driven by snail immune
331 response, we may expect a negative correlation: snails with more effective immune systems may
332 be more likely to successfully trap nematodes in shells while being less likely to harbour active
333 infections. While this would need to be validated, the strength and direction of between- and
334 within-sites correlations between active infections and shell-trapped nematodes may provide
335 useful indicators of the main drivers of snail-nematodes interactions in response to city life.

336 We acknowledge that the relatively small size of our sample does not allow us to draw firm causal
337 conclusions. Nonetheless, we hope our results may encourage larger studies regarding host-
338 parasite interactions in land molluscs in the context of environmental change. As new technical
339 developments such as micro-CT imaging allow non-destructive analyses of snail shells
340 (Falkingham & Rae, 2021), these may extend to using museum and other natural history
341 collections to understand how interactions vary in space and time (Cowlshaw et al., 2019),
342 reaffirming their value for urban ecology and evolution (Shultz et al., 2020).

343 **Author contributions**

344 Initial study idea: MD, DB. Site selection and fieldwork: MD, HR, KDW. Shell data collection: HR,
345 after initial training by MD. Data analysis: MD, after preliminary analyses by HR. Initial manuscript
346 draft: MD. All authors contributed critically to edits and gave final approval for publication.

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351 **Conflict of interest disclosure**

352 The authors declare they have no financial conflict of interest in relation with the content of this
353 article. DB is a recommender for PCI Ecology and PCI Evolutionary Biology.

354 **Data and code availability**

355 Data and R scripts to reproduce all analyses presented in this article, as well as a copy of the
356 Supplementary Materials, are available on Github (<https://github.com/mdahirel/HELICITY->

357 2022_shell-nematodes) and archived in Zenodo (DOI:
358 <https://doi.org/10.5281/zenodo.10794928>).

359 References

360 Alberti M, Correa C, Marzluff JM, Hendry AP, Palkovacs EP, Gotanda KM, Hunt VM, Apgar TM,
361 Zhou Y (2017) Global urban signatures of phenotypic change in animal and plant populations.
362 *Proceedings of the National Academy of Sciences*, 201606034.
363 <https://doi.org/10.1073/pnas.1606034114>

364 Andrus PS, Rae R, Wade CM (2022). Nematodes and trematodes associated with terrestrial
365 gastropods in Nottingham, England. *Journal of Helminthology*, **96**, e81.
366 <https://doi.org/10.1017/S0022149X22000645>

367 Aziz NAA, Daly E, Allen S, Rowson B, Greig C, Forman D, Morgan ER (2016) Distribution of
368 *Angiostrongylus vasorum* and its gastropod intermediate hosts along the rural–urban gradient in
369 two cities in the United Kingdom, using real time PCR. *Parasites & Vectors*, **9**, 56.
370 <https://doi.org/10.1186/s13071-016-1338-3>

371 Barbato D, Benocci A, Caruso T, Manganelli G (2017) The role of dispersal and local environment
372 in urban land snail assemblages: an example of three cities in Central Italy. *Urban Ecosystems*, **20**,
373 919–931. <https://doi.org/10.1007/s11252-017-0643-8>

374 Barber I, Dingemanse NJ (2010) Parasitism and the evolutionary ecology of animal personality.
375 *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 4077–4088.
376 <https://doi.org/10.1098/rstb.2010.0182>

377 Barker GM (Ed.) (2004) *Natural enemies of terrestrial molluscs*. CABI, Wallingford, UK.

378 Bjornstad ON (2022) R package ncf: Spatial covariance functions.

379 Brooks M E., Kristensen K, Benthem K J., van, Magnusson A, Berg C W., Nielsen A, Skaug H J.,
380 Mächler M, Bolker B M. (2017) GlimmTMB balances speed and flexibility among packages for zero-
381 inflated generalized linear mixed modeling. *The R Journal*, **9**, 378. [https://doi.org/10.32614/RJ-](https://doi.org/10.32614/RJ-2017-066)
382 [2017-066](https://doi.org/10.32614/RJ-2017-066)

383 Cain AJ (1988) The scoring of polymorphic colour and pattern variation and its genetic basis in
384 molluscan shells. *Malacologia*, **28**, 1–15.

385 Callomon P (2019) *Standard views for imaging mollusk shells*. American Malacological Society.

386 Cameron R (2008) *Land Snails in the British Isles*. FSC Publications, Telford, UK.

387 Coaglio AL, Ferreira MAND, dos Santos Lima W, de Jesus Pereira CA (2018) Identification of a
388 phenoloxidase- and melanin-dependent defence mechanism in *Achatina fulica* infected with
389 *Angiostrongylus vasorum*. *Parasites & Vectors*, **11**, 113. [https://doi.org/10.1186/s13071-018-](https://doi.org/10.1186/s13071-018-2710-2)
390 [2710-2](https://doi.org/10.1186/s13071-018-2710-2)

391 Cote J, Bestion E, Jacob S, Travis J, Legrand D, Baguette M (2017) Evolution of dispersal strategies
392 and dispersal syndromes in fragmented landscapes. *Ecography*, **40**, 56–73.
393 <https://doi.org/10.1111/ecog.02538>

394 Cowlshaw RM, Andrus P, Rae R (2019) An investigation into nematodes encapsulated in shells of
395 wild, farmed and museum specimens of *Cornu aspersum* and *Helix pomatia*. *Journal of*
396 *Conchology*, **43**, 385–392.

397 Dahirel M, Proux M, Gérard C, Ansart A (2022) Morph-dependent nematode infection and its
398 association with host movement in the land snail *Cepaea nemoralis* (Mollusca, Gastropoda).
399 *Journal of Zoology*, **318**, 181–192. <https://doi.org/10.1111/jzo.13012>

400 Dahirel M, Séguret A, Ansart A, Madec L (2016) Dispersal-related traits of the snail *Cornu*
401 *aspersum* along an urbanisation gradient: maintenance of mobility across life stages despite high
402 costs. *Urban Ecosystems*, **19**, 1847–1859. <https://doi.org/10.1007/s11252-016-0564-y>

403 Daniels RR, Beltran S, Poulin R, Lagrue C (2013) Do parasites adopt different strategies in different
404 intermediate hosts? Host size, not host species, influences *Coitocaecum parvum* (Trematoda) life
405 history strategy, size and egg production. *Parasitology*, **140**, 275–283.
406 <https://doi.org/10.1017/S0031182012001564>

407 Diamond SE, Martin RA (2021) Evolution in cities. *Annual Review of Ecology, Evolution, and*
408 *Systematics*, **52**, 519–540. <https://doi.org/10.1146/annurev-ecolsys-012021-021402>

409 Eötvös CB, Magura T, Lövei GL (2018) A meta-analysis indicates reduced predation pressure with
410 increasing urbanization. *Landscape and Urban Planning*, **180**, 54–59.
411 <https://doi.org/10.1016/j.landurbplan.2018.08.010>

412 Eurostat (European Commission) (2021) *Applying the degree of urbanisation: a methodological*
413 *manual to define cities, towns and rural areas for international comparisons : 2021 edition*.
414 Publications Office of the European Union, LU.

415 Ezenwa VO, Archie EA, Craft ME, Hawley DM, Martin LB, Moore J, White L (2016) Host behaviour–
416 parasite feedback: an essential link between animal behaviour and disease ecology. *Proceedings*
417 *of the Royal Society B: Biological Sciences*, **283**, 20153078.
418 <https://doi.org/10.1098/rspb.2015.3078>

419 Falkingham P, Rae R (2021) 3D morphology of nematode encapsulation in snail shells, revealed
420 by micro-CT imaging. *Scientific Reports*, **11**, 2523. <https://doi.org/10.1038/s41598-021-82106-6>

421 Falkner G, Obrdlik P, Castella E, Speight MCD (2001) *Shelled Gastropoda of western Europe*.
422 Friedrich Held Gesellschaft, München, Germany.

423 Fenoglio MS, Rossetti MR, Videla M (2020) Negative effects of urbanization on terrestrial
424 arthropod communities: a meta-analysis. *Global Ecology and Biogeography*, **29**, 1412–1429.
425 <https://doi.org/10.1111/geb.13107>

426 Fox J, Weisberg S (2019) *An R Companion to Applied Regression*. Sage, Thousand Oaks, CA.

- 427 Furuta E, Yamaguchi K (2001) Haemolymph: blood cell morphology and function. In: *The biology*
428 *of terrestrial molluscs* (ed Barker GM), pp. 289–306. CABI, Wallingford, UK.
- 429 Gámez S, Potts A, Mills KL, Allen AA, Holman A, Randon PM, Linson O, Harris NC (2022) Downtown
430 diet: a global meta-analysis of increased urbanization on the diets of vertebrate predators.
431 *Proceedings of the Royal Society B: Biological Sciences*, **289**, 20212487.
432 <https://doi.org/10.1098/rspb.2021.2487>
- 433 Gérard C, De Tombeur Y, Dahirel M, Ansart A (2023) Land snails can trap trematode cercariae in
434 their shell: Encapsulation as a general response against parasites? *Parasite*, **30**, 1.
435 <https://doi.org/10.1051/parasite/2023001>
- 436 Giannelli A, Cantacessi C, Colella V, Dantas-Torres F, Otranto D (2016) Gastropod-borne
437 helminths: a look at the snail–parasite interplay. *Trends in Parasitology*, **32**, 255–264.
438 <https://doi.org/10.1016/j.pt.2015.12.002>
- 439 Gong X, Qiao Z, Yao H, Zhao D, Eisenhauer N, Scheu S, Liang C, Liu M, Zhu Y-G, Sun X (2024)
440 Urbanization simplifies soil nematode communities and coincides with decreased ecosystem
441 stability. *Soil Biology and Biochemistry*, **190**, 109297.
442 <https://doi.org/10.1016/j.soilbio.2023.109297>
- 443 Hodges MN, McKinney ML (2018) Urbanization impacts on land snail community composition.
444 *Urban Ecosystems*, **21**, 721–735. <https://doi.org/10.1007/s11252-018-0746-x>
- 445 Horsák M, Lososová Z, Čejka T, Juříčková L, Chytrý M (2013) Diversity and biotic homogenization
446 of urban land-snail faunas in relation to habitat types and macroclimate in 32 Central European
447 cities. *PLOS ONE*, **8**, e71783. <https://doi.org/10.1371/journal.pone.0071783>
- 448 iNaturalist contributors, iNaturalist (2024) iNaturalist Research-grade Observations.
449 iNaturalist.org. Occurrence dataset. <https://doi.org/10.15468/ab3s5x>
- 450 Jaffuel G, Půža V, Hug A-S, Meuli RG, Nermuť J, Turlings TCJ, Desurmont GA, Campos-Herrera R
451 (2019) Molecular detection and quantification of slug parasitic nematodes from the soil and their
452 hosts. *Journal of Invertebrate Pathology*, **160**, 18–25. <https://doi.org/10.1016/j.jip.2018.11.005>
- 453 Joint Research Centre (European Commission) (2023) *GHSL data package 2023*. Publications
454 Office of the European Union, LU.
- 455 Jones JS, Leith BH, Rawlings P (1977) *Polymorphism in Cepaea: a problem with too many*
456 *solutions?* *Annual Review of Ecology and Systematics*, **8**, 109–143.
- 457 Kerstes NAG, Breeschoten T, Kalkman VJ, Schilthuizen M (2019) Snail shell colour evolution in
458 urban heat islands detected via citizen science. *Communications Biology*, **2**, 264.
459 <https://doi.org/10.1038/s42003-019-0511-6>
- 460 Korányi D, Egerer M, Rusch A, Szabó B, Batáry P (2022) Urbanization hampers biological control
461 of insect pests: A global meta-analysis. *Science of The Total Environment*, **834**, 155396.
462 <https://doi.org/10.1016/j.scitotenv.2022.155396>

463 Kramarenko S (2014) [Active and passive dispersal of terrestrial mollusks: a review](#). *Ruthenica*, **24**,
464 1–14.

465 Lenth R (2023) [emmeans: estimated marginal means, aka least-squares means \(R package\)](#).

466 Liang H, He Y-D, Theodorou P, Yang C-F (2023) The effects of urbanization on pollinators and
467 pollination: A meta-analysis. *Ecology Letters*, **26**, 1629–1642. <https://doi.org/10.1111/ele.14277>

468 Li X, Liu T, Li H, Geisen S, Hu F, Liu M (2022) Management effects on soil nematode abundance
469 differ among functional groups and land-use types at a global scale. *Journal of Animal Ecology*,
470 **91**, 1770–1780. <https://doi.org/10.1111/1365-2656.13744>

471 Lososová Z, Horsák M, Chytrý M, Čejka T, Danihelka J, Fajmon K, Hájek O, Juříčková L, Kintrová K,
472 Láníková D, Otýpková Z, Řehořek V, Tichý L (2011) Diversity of Central European urban biota:
473 effects of human-made habitat types on plants and land snails. *Journal of Biogeography*, **38**,
474 1152–1163. <https://doi.org/10.1111/j.1365-2699.2011.02475.x>

475 Manoli G, Fatichi S, Schläpfer M, Yu K, Crowther TW, Meili N, Burlando P, Katul GG, Bou-Zeid E
476 (2019) Magnitude of urban heat islands largely explained by climate and population. *Nature*, **573**,
477 55–60. <https://doi.org/10.1038/s41586-019-1512-9>

478 Martin E, El-Galmady S, Johnson MTJ (2024) Urban socioeconomic variation influences the
479 ecology and evolution of trophic interactions. *Ecology Letters*, **27**, e14407.
480 <https://doi.org/10.1111/ele.14407>

481 McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals.
482 *Urban Ecosystems*, **11**, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>

483 Minias P (2023) The effects of urban life on animal immunity: Adaptations and constraints. *Science
484 of The Total Environment*, **895**, 165085. <https://doi.org/10.1016/j.scitotenv.2023.165085>

485 Morand S, Wilson MJ, Glen DM (2004) Nematodes (Nematoda) parasitic in terrestrial molluscs.
486 In: *Natural enemies of terrestrial molluscs* (ed Barker GM), pp. 525–557. CABI, Wallingford, UK.

487 Moreno-Monroy AI, Schiavina M, Veneri P (2021) Metropolitan areas in the world. Delineation
488 and population trends. *Journal of Urban Economics*, **125**, 103242.
489 <https://doi.org/10.1016/j.jue.2020.103242>

490 Murray MH, Sánchez CA, Becker DJ, Byers KA, Worsley-Tonks KE, Craft ME (2019) City sicker? A
491 meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment*, **17**,
492 575–583. <https://doi.org/10.1002/fee.2126>

493 Nakagawa S, Johnson PCD, Schielzeth H (2017) The coefficient of determination R^2 and intra-class
494 correlation coefficient from generalized linear mixed-effects models revisited and expanded.
495 *Journal of The Royal Society Interface*, **14**, 20170213. <https://doi.org/10.1098/rsif.2017.0213>

- 496 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized
497 linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
498 <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- 499 Oosterhoff LM (1977) Variation in growth rate as an ecological factor in the landsnail *Cepaea*
500 *nemoralis* (L.). *Netherlands Journal of Zoology*, **27**, 1–132.
501 <https://doi.org/10.1163/002829677X00072>
- 502 Özgo M (2009) Current problems in the research of *Cepaea* polymorphism. *Folia Malacologica*,
503 **16**, 55–60. <https://doi.org/10.12657/folmal.016.009>
- 504 Parris KM (2016) *Ecology of urban environments*. Wiley-Blackwell, Chichester, UK.
- 505 Pebesma E (2018) Simple features for R: standardized support for spatial vector data. *The R*
506 *Journal*, **10**, 439. <https://doi.org/10.32614/RJ-2018-009>
- 507 Pesaresi M, Politis P (2023) GHS-BUILT-S R2023A - GHS built-up surface grid, derived from
508 Sentinel2 composite and Landsat, multitemporal (1975-2030).
509 <https://doi.org/10.2905/9F06F36F-4B11-47EC-ABB0-4F8B7B1D72EA>
- 510 Piano E, Souffreau C, Merckx T, Baardsen LF, Backeljau T, Bonte D, Brans KI, Cours M, Dahirel M,
511 Debortoli N, Decaestecker E, Wolf KD, Engelen JMT, Fontaneto D, Gianuca AT, Govaert L,
512 Hanashiro FTT, Higuti J, Lens L, Martens K, Matheve H, Matthysen E, Pinseel E, Sablon R, Schön I,
513 Stoks R, Doninck KV, Dyck HV, Vanormelingen P, Wichelen JV, Vyverman W, Meester LD,
514 Hendrickx F (2020) Urbanization drives cross-taxon declines in abundance and diversity at
515 multiple spatial scales. *Global Change Biology*, **26**, 1196–1211.
516 <https://doi.org/10.1111/gcb.14934>
- 517 Pieterse A, Malan AP, Ross JL (2017) Nematodes that associate with terrestrial molluscs as
518 definitive hosts, including *Phasmarhabditis hermaphrodita* (Rhabditida: Rhabditidae) and its
519 development as a biological molluscicide. *Journal of Helminthology*, **91**, 517–527.
520 <https://doi.org/10.1017/S0022149X16000572>
- 521 Pollard E, Cooke AS, Welch JM (1977) The use of shell features in age determination of juvenile
522 and adult Roman snails *Helix pomatia*. *Journal of Zoology*, **183**, 269–279.
523 <https://doi.org/10.1111/j.1469-7998.1977.tb04186.x>
- 524 R Core Team (2023) [R: a language and environment for statistical computing](https://www.R-project.org/).
- 525 Radwan MA, El-Gendy KS, Gad AF (2020) Biomarker responses in terrestrial gastropods exposed
526 to pollutants: A comprehensive review. *Chemosphere*, **257**, 127218.
527 <https://doi.org/10.1016/j.chemosphere.2020.127218>
- 528 Rae R (2017) The gastropod shell has been co-opted to kill parasitic nematodes. *Scientific Reports*,
529 **7**, 4745. <https://doi.org/10.1038/s41598-017-04695-5>

- 530 Rae R (2018) Shell encapsulation of parasitic nematodes by *Arianta arbustorum* (Linnaeus, 1758)
531 in the laboratory and in field collections. *Journal of Molluscan Studies*, **84**, 92–95.
532 <https://doi.org/10.1093/mollus/eyx045>
- 533 Rae R (2023) Avoidance and attraction behaviour of slugs exposed to parasitic nematodes. *Journal*
534 *of Invertebrate Pathology*, **197**, 107896. <https://doi.org/10.1016/j.jip.2023.107896>
- 535 Rae RG, Robertson JF, Wilson MJ (2008) Susceptibility and immune response of *Deroceras*
536 *reticulatum*, *Milax gagates* and *Limax pseudoflavus* exposed to the slug parasitic nematode
537 *Phasmarhabditis hermaphrodita*. *Journal of Invertebrate Pathology*, **97**, 61–69.
538 <https://doi.org/10.1016/j.jip.2007.07.004>
- 539 Rosin ZM, Kwieciński Z, Lesicki A, Skórka P, Kobak J, Szymańska A, Osiejuk TS, Katuski T, Jaskulska
540 M, Tryjanowski P (2018) Shell colour, temperature, (micro)habitat structure and predator
541 pressure affect the behaviour of *Cepaea nemoralis*. *The Science of Nature*, **105**, 35.
542 <https://doi.org/10.1007/s00114-018-1560-2>
- 543 Russo J, Madec L (2011) Dual strategy for immune defense in the land snail *Cornu aspersum*
544 (Gastropoda, Pulmonata). *Physiological and Biochemical Zoology: Ecological and Evolutionary*
545 *Approaches*, **84**, 212–221. <https://doi.org/10.1086/659123>
- 546 Russo J, Madec L (2013) Linking immune patterns and life history shows two distinct defense
547 strategies in land snails (Gastropoda, Pulmonata). *Physiological and Biochemical Zoology*, **86**,
548 193–204. <https://doi.org/10.1086/669482>
- 549 Scheil AE, Hilsmann S, Triebkorn R, Köhler H-R (2013) Shell colour polymorphism, injuries and
550 immune defense in three helicid snail species, *Cepaea hortensis*, *Theba pisana* and *Cornu*
551 *aspersum maximum*. *Results in Immunology*, **3**, 73–78.
552 <https://doi.org/10.1016/j.rinim.2013.06.002>
- 553 Scheil AE, Hilsmann S, Triebkorn R, Köhler H-R (2014) Shell colouration and parasite tolerance in
554 two helicoid snail species. *Journal of Invertebrate Pathology*, **117**, 1–8.
555 <https://doi.org/10.1016/j.jip.2014.01.003>
- 556 Schiavina M, Freire S, Carioli A, MacManus K (2023) GHS-POP R2023A - GHS population grid
557 multitemporal (1975-2030). [https://doi.org/10.2905/2FF68A52-5B5B-4A22-8F40-](https://doi.org/10.2905/2FF68A52-5B5B-4A22-8F40-C41DA8332CFE)
558 [C41DA8332CFE](https://doi.org/10.2905/2FF68A52-5B5B-4A22-8F40-C41DA8332CFE)
- 559 Schiavina M, Melchiorri M, Pesaresi M (2023) GHS-SMOD R2023A - GHS settlement layers,
560 application of the Degree of Urbanisation methodology (stage I) to GHS-POP R2023A and GHS-
561 BUILT-S R2023A, multitemporal (1975-2030). [https://doi.org/10.2905/A0DF7A6F-49DE-46EA-](https://doi.org/10.2905/A0DF7A6F-49DE-46EA-9BDE-563437A6E2BA)
562 [9BDE-563437A6E2BA](https://doi.org/10.2905/A0DF7A6F-49DE-46EA-9BDE-563437A6E2BA)
- 563 Schiavina M, Moreno-Monroy A, Maffenini L, Veneri P (2019) GHS-FUA R2019A - GHS functional
564 urban areas, derived from GHS-UCDB R2019A (2015). [https://doi.org/10.2905/347F0337-F2DA-](https://doi.org/10.2905/347F0337-F2DA-4592-87B3-E25975EC2C95)
565 [4592-87B3-E25975EC2C95](https://doi.org/10.2905/347F0337-F2DA-4592-87B3-E25975EC2C95)

- 566 Segade P, García-Estévez J, Arias C, Iglesias R (2013) Parasitic infections in mixed system-based
567 heliciculture farms: dynamics and key epidemiological factors. *Parasitology*, **140**, 482–497.
568 <https://doi.org/10.1017/S0031182012001795>
- 569 Shultz AJ, Adams BJ, Bell KC, Ludt WB, Pauly GB, Vendetti JE (2020) Natural history collections are
570 critical resources for contemporary and future studies of urban evolution. *Evolutionary*
571 *Applications*, **14**, 233–247. <https://doi.org/10.1111/eva.13045>
- 572 Szulkin M, Munshi-South J, Charmantier A (Eds.) (2020) *Urban Evolutionary Biology*. Oxford
573 University Press. <https://doi.org/10.1093/oso/9780198836841.001.0001>
- 574 Theodorou P (2022) The effects of urbanisation on ecological interactions. *Current Opinion in*
575 *Insect Science*, **52**, 100922. <https://doi.org/10.1016/j.cois.2022.100922>
- 576 Valdés-Correcher E, Popova A, Galmán A, Prinzing A, Selikhovkin AV, Howe AG, Mrazova A,
577 Dulaurent A-M, Hampe A, Tack AJM, Bouget C, Lupaștean D, Harvey D, Musolin DL, Lövei GL,
578 Centenaro G, Halder IV, Hagge J, Dobrosavljević J, Pitkänen J-M, Koricheva J, Sam K, Barbaro L,
579 Branco M, Ferrante M, Faticov M, Tahadlová M, Gossner M, Cauchoix M, Bogdziewicz M,
580 Duduman M-L, Kozlov MV, Bjoern MC, Mamaev NA, Fernandez-Conradi P, Thomas RL, Wetherbee
581 R, Green S, Milanović S, Moreira X, Mellerin Y, Kadiri Y, Castagneyrol B (2022) Herbivory on the
582 pedunculate oak along an urbanization gradient in Europe: Effects of impervious surface, local
583 tree cover, and insect feeding guild. *Ecology and Evolution*, **12**, e8709.
584 <https://doi.org/10.1002/ece3.8709>
- 585 Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Golemund G, Hayes A, Henry
586 L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu
587 V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the Tidyverse. *Journal of*
588 *Open Source Software*, **4**, 1686. <https://doi.org/10.21105/joss.01686>
- 589 Williamson P (1979) Age determination of juvenile and adult *Cepaea*. *Journal of Molluscan*
590 *Studies*, **45**, 52–60.
- 591 Williams AJ, Rae R (2015) Susceptibility of the Giant African snail (*Achatina fulica*) exposed to the
592 gastropod parasitic nematode *Phasmarhabditis hermaphrodita*. *Journal of Invertebrate*
593 *Pathology*, **127**, 122–126. <https://doi.org/10.1016/j.jip.2015.03.012>
- 594 Williams A, Rae R (2016) *Cepaea nemoralis* (Linnaeus, 1758) uses its shell as a defence mechanism
595 to trap and kill parasitic nematodes. *Journal of Molluscan Studies*, **82**, 349–350.
596 <https://doi.org/10.1093/mollus/eyv064>
- 597 Wilson MJ, Hughes LA, Hamacher GM, Glen DM (2000) Effects of *Phasmarhabditis hermaphrodita*
598 on non-target molluscs. *Pest Manag Sci*, **56**, 711–716. [https://doi.org/10.1002/1526-4998\(200008\)56:8%3C711::AID-PS185%3E3.0.CO;2-O](https://doi.org/10.1002/1526-4998(200008)56:8%3C711::AID-PS185%3E3.0.CO;2-O)
- 600 Wilson MJ, Hughes LA, Jefferies D, Glen DM (1999) Slugs (*Deroceras reticulatum* and *Arion ater*
601 agg.) avoid soil treated with the rhabditid nematode *Phasmarhabditis hermaphrodita*. *Biological*
602 *Control*, **16**, 170–176. <https://doi.org/10.1006/bcon.1999.0757>

- 603 Wolda H (1967) The effect of temperature on reproduction in some morphs of the landsnail
604 *Cepaea nemoralis* (L.). *Evolution*, **21**, 117–129. [https://doi.org/10.1111/j.1558-](https://doi.org/10.1111/j.1558-5646.1967.tb00135.x)
605 [5646.1967.tb00135.x](https://doi.org/10.1111/j.1558-5646.1967.tb00135.x)
- 606 Wynne R, Morris A, Rae R (2016) Behavioural avoidance by slugs and snails of the parasitic
607 nematode *Phasmarhabditis hermaphrodita*. *Biocontrol Science and Technology*, **26**, 1129–1138.
608 <https://doi.org/10.1080/09583157.2016.1185513>
- 609 Żbikowska E, Marszewska A, Cichy A, Templin J, Smorąg A, Strzala T (2020) *Cepaea* spp. as a source
610 of *Brachylaima mesostoma* (Digenea: Brachylaimidae) and *Brachylecithum* sp. (Digenea:
611 Dicrocoeliidae) larvae in Poland. *Parasitology Research*, **119**, 145–152.
612 <https://doi.org/10.1007/s00436-019-06516-2>