FOLIA MALACOLOGICA
Folia Malacol. 34(2): 127–141
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, June 2026
https://doi.org/10.12657/folmal.034.013

HABITAT PREFERENCE AND CONSERVATION OF *COCHLICOPA NITENS* (M. VON GALLENSTEIN, 1848) (EUPULMONATA: STYLOMMATOPHORA: COCHLICOPIDAE) IN SWITZERLAND

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Abstract: The ecology of *Cochlicopa nitens* (M. von Gallenstein, 1848) is poorly known, despite its threatened status and extremely rare occurrence throughout Europe. To better understand habitat preferences and assess the vitality of each population, we investigated all nine known sites of *C. nitens* in Switzerland. All populations were located at the unforested parts of different lakeshores or alongside the Rhine River, on a calcareous substrate and with a water conductivity at around 410 μSv. At the habitat scale, we found a preference for *Magnocaricion* habitats and a unimodal relationship with distance to the groundwater level. At the microhabitat scale, high *C. nitens* densities were associated with heterogeneous micro-topography and high moss volume. Our results suggest that *C. nitens* is a highly hygrophilous species with a strong preference for characteristics associated with *Magnocaricion* habitats (primarily *Caricetum elatae*). Sites that are either too dry or too wet are avoided. Micro-topography, mostly resulting from tussock-forming sedges, enables small-scale vertical migration and thus an avoidance of temporal floodings. Large moss volumes retain humidity when water levels are lowering and allow the species to survive drier periods. Thanks to this improved understanding, we discovered seven new sites at Lake Neuchâtel and confirm a total of 16 populations for *C. nitens* in Switzerland.

Keywords: conservation; flooding; Gastropoda; *Magnocaricion*; site management

INTRODUCTION

Cochlicopa nitens (M. von Gallenstein, 1848) is a threatened gastropod species for which research has focused on taxonomy (Armbruster 1994, 1995, Armbruster & Pfenninger 2003, Armbruster & Schlegel 2009), but little is known about its ecology, habitat preference and the needed management practices to conserve its populations.

The continental and disjunct distribution of *C. nitens* ranges from central to eastern Europe and further to central Asia (Welter-Schultes 2012, Orziyeva & Davronov 2024). Gastropod-identification guide books list periodically flooded swamps, very moist meadows, and wet forests on calcareous substrates as broad habitats (Kerney et al. 1983, Welter-Schultes 2012, von Proschwitz et al. 2023, Wiese 2024). More detailed reports exist in Sweden (von Proschwitz 1998, 2006a, 2006b, 2007, ArtDatabanken 2026), where the species inhabits ash-dominated flooded forests, various types of swamps and calcareous fens with high humidity and stable hydrology. In Finland, it was found in the treeless part of a fen with sparsely growing *Alnus glu-*

tinosa bushes, dominated by *Phragmites australis* and *Carex* spp. (Ormio et al. 2016). In France, *C. nitens* was reported from a natural reserve comprising a flooded forest next to the Rhine River and from small calcareous and oligotrophic swamps, where it was collected from the litter and observed under logs (Cucherat & Boca 2005).

Due to its rather wide distribution (E. Neubert, pers. comm. 2025), *C. nitens* is categorised "least concern" (LC) in the European Red List of Terrestrial Molluscs (Neubert et al. 2019). On a more regional scale however, *C. nitens* is rare throughout its entire range (Kerney et al. 1983, Welter-Schultes 2012). National red lists depict high extinction risks: *C. nitens* is "critically endangered" (CR) in the Czech Republic (Farkač et al. 2005) and Germany (Jungbluth & von Knorre 2011), "endangered" (EN) in Austria (Reischütz & Reischütz 2007) and Sweden (Eide 2020) and "data deficient" (DD) in France (Prié et al. 2021). In Sweden, there has been an ongoing process of decline for several decades: on the island of Gotland in the Baltic Sea – one of the former strongholds of *C. nitens* – at revisits (1997–2017) of all its earlier known localities from the 1920s-1940s, it had disappeared from 20 of the former 25 occurrences, corresponding to an 80% decline (von Proschwitz 1998, 2010, unpublished data). In other Swedish areas, the decline was also noticeable and the species totally disappeared from 35 of 54 former localities (63%) (ArtDatabanken 2026, von Proschwitz unpublished data). In the Czech Republic, Ložek (1958) claimed an "obvious decline" of the species already decades ago, based on the destruction and degradation of its habitats. He further supports this by the fact that the species' optimum occurred in the early Holocene, when calcareous swamps were much more prevalent in Central Europe (Ložek 1958). Considering these findings, the species' status in the European Red List will be upgraded to at least "near threatened" (NT) in the upcoming revision (E. Neubert, pers. comm. 2025).

In line with its rarity and long-term declines, *C. nitens* is also considered one of the most endangered terrestrial gastropod species in Switzerland. It is categorised CR in the Swiss Red List (Turner et al. 1998, Rüetschi et al. 2012) and is a national priority (NP) species for conservation measures (BAFU 2025). At the beginning of 2025, a total of nine populations of *C. nitens* were known in Switzerland, of which seven are located at or close to lakeshores (Lake Dittlig, Lake Neuchâtel, Lake Thun), and two next to the Rhine River. Some of the populations had not been visited for years and their status and extinction potential remained uncertain.

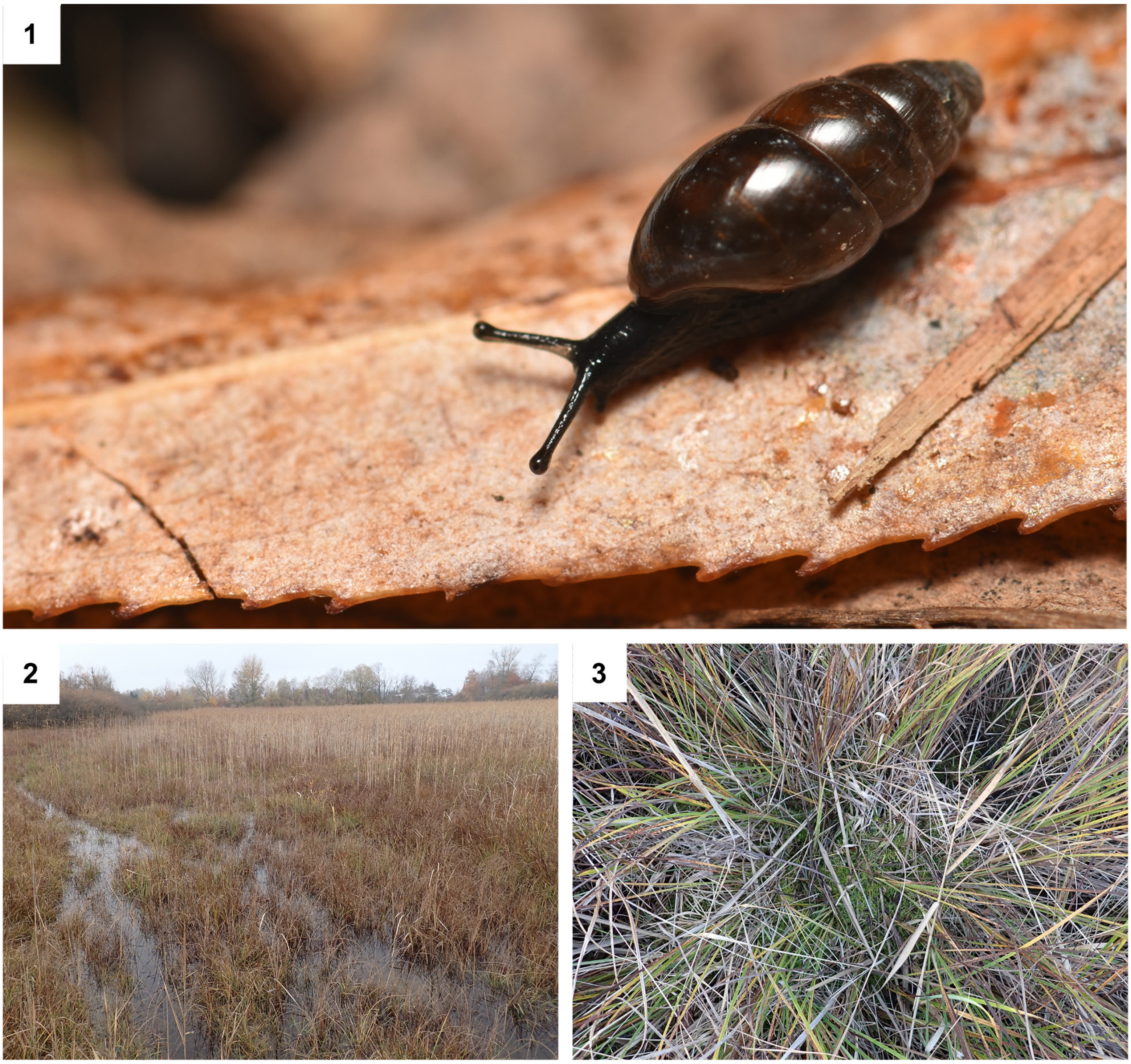
The aim of the study was to 1) analyse the habitat preferences of *C. nitens* in Switzerland; 2) identify environmental factors with high population vitality of *C. nitens*; and 3) search for new, previously unknown populations in Switzerland based on the knowledge gained from the first two steps.

MATERIAL AND METHODS

FIELD SAMPLING AT THE HABITAT SCALE

We visited all nine Swiss populations of *C. nitens* between mid-October and mid-November 2025. At three sites with relatively large populations of *C. nitens* (nos. 1, 3 and 4 in Fig. 4), we investigated the habitat and groundwater level preference by surveying *C. nitens* in systematic sampling grids. As all three sites are nature protected areas, we used the boundaries of the legally protected area to define a grid with 25 m mesh width each. This distance was chosen arbitrarily in QGIS V3.40.14 to ensure a manageable number of intersection points across the entire areas. We derived coordinates from these points and checked them in the field using a submeter-precise GPS (ArduSimple). At each point-coordinate, we searched an area of approximately 1 m^2 and determined the presence or absence of *C. nitens*. For this purpose, we lifted and removed litter and moss and checked the vegetation basis by eye and with the help of a headlamp. We spent at least three minutes before registering an absence. Although some inaccessible sites had to be abandoned during sampling (e.g. small offshore islands, too dense reed vegetation), we checked a total of 600 point-coordinates in the field (160 in site no. 1, 289 in site no. 3, 151 in site no. 4). In addition, we mapped the habitats of the three sites following the habitat-typology "TypoCH", the standard for vegetation assessments in Switzerland (Delarze et al. 2015).

We then intersected all 600 presence or absence point-coordinates with the digital elevation model (DEM) "swissALTI3D", a precise raster layer with altitude estimates at 0.5 m resolution (swisstopo 2024), and the TypoCH-habitat-mapping. Because all three sites are very close to lakeshores, we assumed the lake water level to be an adequate proxy for the groundwater level at each study site. To gain the approximate distance to the groundwater level for all 600 datapoints, we therefore subtracted the measurement of the water level of the corresponding lake on the day of sampling (BAFU 2026, Lake Thun for site no. 1, Lake Neuchâtel for site no. 3 and 4) from the altitude obtained by the DEM.



Figs 1–3. *Cochlicopa nitens* in Switzerland: 1 – a specimen; 2 – its habitat; 3 – and microhabitat

FIELD SAMPLING AT THE MICROHABITAT SCALE

We assessed the vitality of all *C. nitens* populations in Switzerland by counting the individuals occurring in square plots of 0.5 × 0.5 m size (quadrat method, Cameron & Pokryszko 2005) within the species' habitat. Depending on the extent of each population, we randomly defined 3–10 replicates (total n = 53). To avoid too many absences at this scale, the criteria for the plot definition were a minimum presence of one living or dead (empty shells) individual and an adequate coverage of the extension of the population. After searching the vegetation, we cut and removed it to search the litter, moss and vegetation basis for *C. nitens* individuals by eye. We beat the cut biomass onto a white and flat bowl to detect also climbing individuals (Figs S1–S4). To avoid double-counting, we removed every inspected individual from the plot. We distinguished living vs. dead and juvenile vs. adult individuals in the counting.

We are aware that this methodological approach is limited by varying detectability depending on microhabitats, as well as by the fact that individuals may be buried in the soil during dry periods or in winter. For this reason, we conducted all surveys within a short time period of four weeks and attempted to standardise our sampling effort. In line with Książkiewicz-Parulska & Gołdyn (2017) we chose a non-lethal method to get a time-effective in situ estimation of the vitality of each population, whilst minimising potential detrimental effects on the populations of this highly endangered gastropod species.

In addition to the vitality assessment, we determined the following environmental variables for each plot: cover (%) and volume (L) of litter and moss, list of occurring plant species and their percentage cover, number of living reed stalks, distance to the nearest *Salix*-shrubs, distance to the groundwater, pH and water conductivity (using the Hi98129 Hanna instruments). Because the distance to the groundwater can vary with topography and vegetation structure within a plot, we measured it at all four corners and in the middle of each plot, resulting in five measurements per plot. Where needed, we drilled a hole in the soil to reach the groundwater. In order to stabilise the hydrology after the drilling, we waited at least 30 minutes before measuring the distance to the five points. From the list of plant species, we derived average ecological indicator values (EIVs for moisture, temperature, nutrients, pH and mowing-tolerance, Landolt et al. 2010). Moreover, we assessed the species richness of all living, accompanying terrestrial gastropod species.

Following the investigation of the ecological requirements of *C. nitens*, we invested six field days to search for previously unknown populations. We focused on the most promising areas depicting the corresponding habitats and located in proximity to the known populations. We spent three days at Lake Thun (Seeallmend, Weissenau), two days at Lake Neuchâtel (whole extent along the southern lakeshore) and one day in the surroundings of Lake Dittlig (Lake Amsoldingen, Lake Übeschi, Geistsee, Waldweier). Furthermore, we invested one day at Lake Burgäschi, where the species was last recorded in 1949.

STATISTICAL ANALYSES

On the habitat scale, we estimated the probability of occurrence of *C. nitens* using a binomial generalised linear model (GLM) with distance to groundwater, habitat type and site as dependent variables. Because we expected an optimum with respect to distance to the groundwater, we included a quadratic term in the model.

On the microhabitat scale, we considered the number and proportion of living individuals (adults plus juveniles) and the proportion of only juvenile living individuals as vitality measures of every *C. nitens* population. Prior to analysis, all environmental variables were z-transformed, log10-transformed or square-root-transformed and checked for pairwise correlations. Volume and cover estimate for moss and litter were highly correlated, and we only used volume in the analyses. Furthermore, the EIVs (with the exception of mowing-tolerance) and litter volume were excluded from the analysis, because the EIVs were highly correlated with one another, and litter volume was strongly negatively correlated with moss volume. We included all remaining environmental variables (moss volume, number of living reed stalks, cover of *Carex elata*, distance to the nearest *Salix*-shrubs, pH, water conductivity, groundwater level distance [mean and standard deviation], EIV for mowing tolerance) and the gastropod species richness in the model selection for the vitality measures. We added quadratic terms where we expected an optimum. To account for the nested sampling design, we performed generalised linear mixed-effect models (GLMM) using the lme4 package (Bates et al. 2015) and with study site as random factor. We used a negative binomial distribution (function glmer.nb) for modelling the number of living individuals to address over-dispersion of the count data. For the proportion of living and juvenile individuals we used a Gaussian distribution (function lmer). Model selection was performed using the dredge function from the MuMIn R-package (Bartoń 2010), ranking models by the Akaike's Information Criterion corrected for small sample size (AICc). The explained variation of the final models (marginal pseudo-R^2 and conditional pseudo-R^2) was computed with the r.squaredGLMM function of the MuMIn R-package (Bartoń 2010). We checked the residuals of the best model for model violation using the DHARMa R-package (Hartig 2016). All of our models fitted the data well. We performed all analyses using R version 4.2.3 (R Core Team 2023).

RESULTS

HABITAT SCALE

We confirmed an occurrence of *C. nitens* for 126 out of 600 point-coordinates (21%) checked in the field (inset maps in Fig. 4). The binomial GLM showed significant effects for both habitat types (Table S1, χ^2 = 14.86, p = 0.002) and groundwater level distance (χ^2 = 3.70, p = 0.054 for the quadratic term). When we excluded habitat type from the model, the effect of the groundwater level distance increased in importance (χ^2 = 10.15, p = 0.001).

With 71% of all occurrences in *Magnocaricion* (TypoCH 2.2.1), *C. nitens* showed a clear preference for this habitat type (Fig. 5), whose vegetation was mostly dominated by the tussock-forming sedge *Carex elata* (*Magnocaricion* type *Caricetum elatae)* and often accompanied by *Phragmites australis, Galium palustre* and *Mentha aquatica* (complete list in

Table S3). In some sites, *Carex elata* was occasionally replaced by other sedges such as *C. riparia* or *C. appropinquata*. The second important habitat was *Phragmition* (TypoCH 2.1.2), which was characterised by the domination of reed (*Phragmites australis*). Less important habitats were *Caricion davalliane* (TypoCH 2.3.1) and *Molinion* (TypoCH 2.2.3).

For the groundwater level distance, the modelled occurrence probability of *C. nitens* revealed a unimodal relationship with highest probabilities at 24.1, 23.3 and 23.8 cm distance, respectively (Fig. 6).

MICROHABITAT SCALE

Over all nine Swiss populations of *C. nitens*, we estimated an average density of 27.7 ± 5.7 living individuals per 0.25 m². The two populations next to the Rhine River (sites nos. 8 and 9) showed the lowest densities with only one individual, while the ones at Lake Neuchâtel revealed the highest densities with up to 175 individuals per 0.25 m². The average densities of living adults and juveniles were 15.3 ± 3.6 and 12.4 ± 2.4 individuals per 0.25 m², respectively. The proportion of living individuals averaged at 77%, the one for living juvenile individuals at 34%. All vitality measures are summarised in Table 1.

The overall means for the 53 investigated plots from all the nine sites showed a characterisation by little distance to the groundwater level (overall average of 4.3 cm), alkaline pH (6.8), intermediate water conductivity (411 µS/cm), high litter and moss volumes (1.6 and 1.5 L per 0.25 m²), high *Carex elata* cover (45%), rather low reed density (12 stalks per 0.25 m²) and an intermediate mowing tolerance (EIV of 3.0 on a scale from 1–5). In line with the results at the habitat scale, most of the 53 randomly chosen plots were located in *Magnocaricion* (TypoCH 2.2.1, 86.8%), followed by *Phragmition* (TypoCH 2.1.2, 11.3%) and *Molinion* (TypoCH 2.3.1, 1.9%). Furthermore, they were rather distant to the nearest *Salix*-shrubs (on average 37 m) in the open parts of the fens, and all sites were located at relatively low altitude (395 to 652 m a.s.l.). *C. nitens* was accompanied by other hygrophilous gastropod species includ-

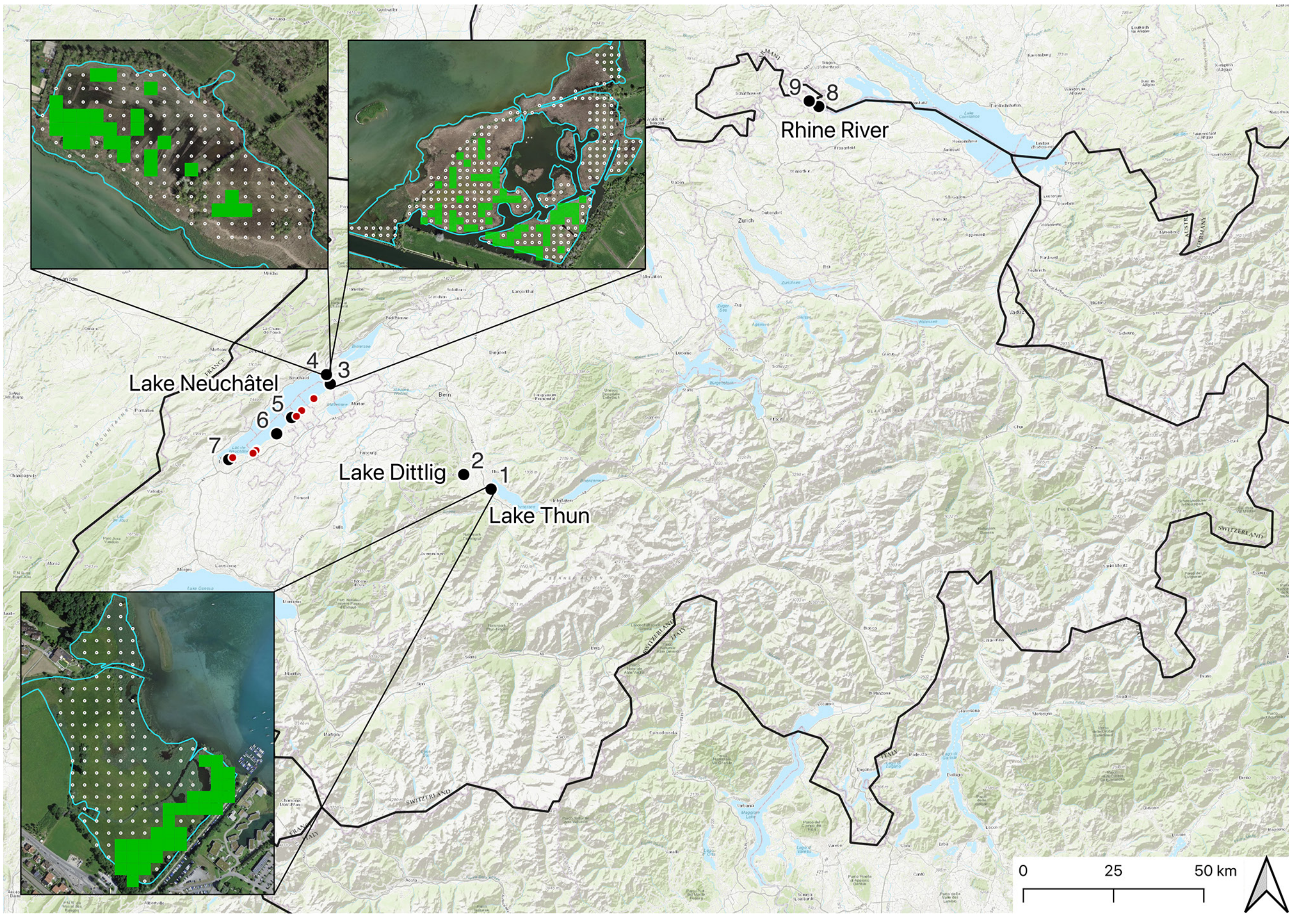


Fig. 4. Distribution of all nine investigated sites of *Cochlicopa nitens* in Switzerland, known by the beginning of 2025. Presence-absence surveys ("habitat scale") were conducted in systematic grids of 25 m at sites nos. 1, 3, and 4 and are displayed with the small inset maps (green = presence, white = absence, blue lines = nature protection areas). Density-estimations ("microhabitat scale") were conducted at all sites. Later in the year, more sites along the southern lakeshore of Lake Neuchâtel were discovered (red small dots)

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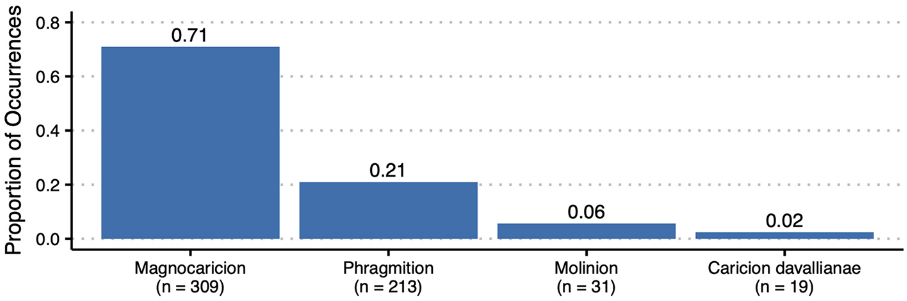

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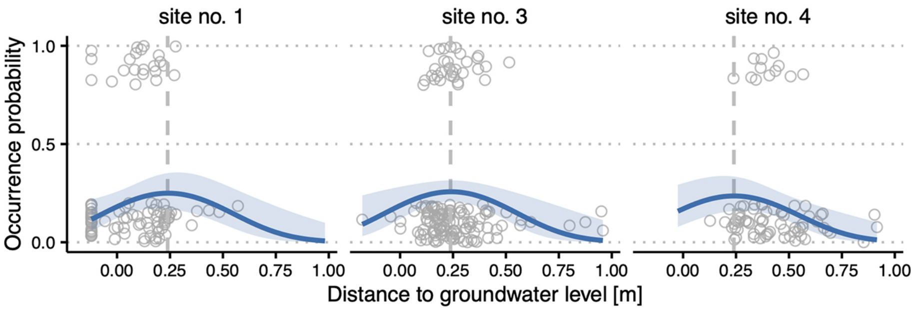

Figs 5–6. Results of the systematic presence–absence survey of *Cochlicopa nitens* conducted using 25 m grid cells at three sites with large populations (nos. 1, 3 and 4). In total, 600 point-coordinates were surveyed in the field: 5 – the 124 recorded presences of *C. nitens*, the majority occurred in TypoCH 2.1.1 *Magnocaricion* habitats (71%), followed by 2.1.2 *Phragmition* (21%), 2.3.1. *Molinion* (6%) and 2.2.3 *Caricion davallianae* (2%). Only habitat types with more than 10 occurrences are shown; 6 – the probability of occurrence of *C. nitens* exhibited a unimodal response along the groundwater level gradient, with site-specific optima at 24.1, 23.3, and 23.8 cm, respectively (dashed vertical line). For each site, the fitted regression line and the corresponding 95% confidence interval derived from a generalised linear model (GLM) along with the raw data points in grey are shown

ing *Vertigo antivertigo* (92.5% of all plots), *Euconulus alderi* (81.1%) and *Zonitoides nitidus* (73.6%). A more detailed descriptive statistic of the environmental variables is summarised in Table 2 and the full list of accompanying gastropod and plant species can be found in Tables S2 and S3.

The model selection for the number of living individuals revealed a model including moss volume, water conductivity, variation in groundwater level distance and gastropod species richness as important and significant predictors of *C. nitens* density (Fig. 7, Table 3). The model explained 51.1% (marginal pseudo-R^2) and 73.2% (conditional pseudo-R^2) of the variation in the density of *C. nitens*, respectively. The other variables did not substantially explain the density of *C. nitens* and were not part of the final model. The next best models were significantly worse with a ΔAIC > 2.0.

Table 1. Vitality measures of the nine studied populations of *Cochlicopa nitens* in Switzerland. In addition to the quantitative measures from the plots, the number of surveyed plots (n) and estimated area (ha) of the species' occurrence is indicated for each site

Site	n	area (ha)	Living Ind.			Prop. living Ind.			Prop. living juvenile Ind.		
			mean	min.	max.	mean	min.	max.	mean	min.	max.
1	10	1.9	28.1	3.0	92.0	0.9	0.7	1.0	0.5	0.3	0.8
2	6	0.1	5.5	0.0	19.0	0.7	0.0	1.0	0.2	0.0	0.3
3	10	4.2	31.7	1.0	121.0	0.9	0.8	1.0	0.5	0.0	0.8
4	8	1.8	17.1	2.0	34.0	0.7	0.2	1.0	0.6	0.0	1.0
5	4	0.9	121.5	25.0	175.0	1.0	0.9	1.0	0.4	0.3	0.5
6	4	8.4	8.8	3.0	24.0	0.8	0.6	1.0	0.7	0.5	0.8
7	4	0.4	42.8	5.0	118.0	0.8	0.4	1.0	0.3	0.3	0.4
8	3	0.1	1.0	0.0	2.0	0.6	0.0	1.0	0.0	0.0	0.0
9	4	0.3	1.0	1.0	1.0	0.2	0.1	0.5	0.3	0.0	1.0

For the proportion of living individuals and the proportion of living juvenile individuals, none of the predictors we tested improved the model. The null model, containing only the intercept, described the data best according to the model selection.

The search for new, unknown populations was successful at Lake Neuchâtel, where we could find seven new populations of *C. nitens* along the whole extent of the southern lakeshore, where extensive *Magnocaricion*-habitats prevail in close proximity to the groundwater level. At Lake Thun and the smaller lakes in the vicinity of Lake Dittlig, we could not find any new populations, despite the presence of at least small-scaled, seemingly suitable habitats. Ultimately, we could not confirm the species' presence at Lake Burgäschi.

Table 2. Descriptive statistics of the environmental variables for all nine studied sites of *Cochlicopa nitens* in Switzerland

Environmental variable		Site									Overall mean
		1	2	3	4	5	6	7	8	9	
Altitude [m a.s.l.]	–	558	652	430	430	430	430	430	396	395	461.2
Litter volume [L]	mean	1.5	1.8	1.4	2.0	0.6	1.0	2.0	0.4	3.3	1.6
	min.	0.2	1.4	0.0	0.5	0.1	0.5	0.2	0.1	1.2	0.5
	max.	3.8	2.2	4.6	3.4	1.3	1.4	4.4	0.8	5.2	3.0
Moss volume [L]	mean	2.2	0.2	2.1	1.3	2.0	1.5	1.4	2.6	0.0	1.5
	min.	0.2	0.0	0.0	0.5	1.8	0.4	0.1	1.8	0.0	0.5
	max.	6.5	0.6	5.6	2.6	2.0	2.7	2.4	3.4	0.1	2.9
pH	mean	6.3	6.1	6.7	6.8	7.3	7.0	7.0	6.7	7.7	6.8
	min.	5.8	5.7	6.1	6.6	6.9	6.8	6.8	6.6	7.6	6.6
	max.	6.8	6.8	7.3	7.1	7.6	7.3	7.2	6.8	7.9	7.2
Water conductivity [μSv]	mean	294.6	362.0	436.4	527.5	411.5	368.5	382.5	679.7	234.0	410.7
	min.	141.0	178.0	129.0	310.0	287.0	208.0	334.0	499.0	98.0	242.7
	max.	653.0	661.0	998.0	790.0	547.0	485.0	416.0	820.0	365.0	637.2
Groundwater level distance [cm]	mean	4.2	5.7	9.3	4.0	−3.0	−4.5	1.0	17.8	>50.0	4.3
	min.	−1.2	4.1	0.5	−7.5	−5.0	−7.8	−2.0	17.1	>50.0	−0.2
	max.	22.4	7.9	24.5	19.6	0.2	−2.5	2.6	19.0	>50.0	11.7
Carex elata cover [%]	mean	29.5	58.3	35.5	35.0	37.5	62.5	72.5	50.0	23.8	45.0
	min.	0.0	20.0	0.0	0.0	10.0	10.0	60.0	30.0	0.0	14.4
	max.	90.0	90.0	75.0	75.0	60.0	90.0	90.0	60.0	75.0	78.3
Distance to nearest shrub [m]	mean	24.2	14.4	84.3	25.5	53.3	63.8	19.9	15.8	29.0	36.7
	min.	0.8	4.5	37.0	1.2	7.0	39.0	6.5	2.8	17.0	12.9
	max.	56.0	20.5	226.0	67.0	120.0	80.0	28.0	22.5	35.0	72.8
Reed density [number of living stalks]	mean	6.8	15.2	14.9	10.0	6.8	2.8	3.5	3.7	44.5	12.0
	min.	0.0	4.0	4.0	2.0	3.0	2.0	1.0	1.0	28.0	5.0
	max.	29.0	32.0	30.0	18.0	10.0	5.0	8.0	7.0	79.0	24.2
Ecological indicator value (EIV): Mowing-tolerance	mean	3.1	2.7	3.2	3.2	2.9	3.2	3.1	3.2	2.8	3.0
	min.	2.5	2.5	2.5	2.0	2.8	3.2	3.0	3.0	2.5	2.7
	max.	4.0	3.0	4.5	4.7	3.0	3.3	3.3	3.4	3.3	3.6
Ecological indicator value (EIV): Temperature	mean	3.7	3.6	3.7	3.7	3.8	3.6	3.5	3.5	3.8	3.6
	min.	3.6	3.4	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5
	max.	3.8	3.8	3.8	4.0	3.9	3.7	3.5	3.6	4.0	3.8
Ecological indicator value (EIV): Moisture	mean	4.7	4.5	4.5	4.5	4.6	4.6	4.5	4.3	4.4	4.5
	min.	4.4	4.0	4.1	4.2	4.5	4.5	4.5	4.3	3.7	4.2
	max.	4.8	4.8	4.8	5.0	4.6	4.7	4.5	4.4	4.8	4.7
Ecological indicator value (EIV): Alkality	mean	3.2	3.1	3.3	3.1	3.3	3.1	3.0	3.2	3.0	3.1
	min.	3.0	3.0	3.0	2.8	3.0	3.0	3.0	3.0	3.0	3.0
	max.	3.5	3.3	3.5	3.5	3.4	3.3	3.0	3.3	3.0	3.3
Ecological indicator value (EIV): Light	mean	3.4	3.4	3.4	3.4	3.3	3.4	3.3	3.4	3.3	3.4
	min.	3.0	3.3	3.0	3.0	3.3	3.3	3.3	3.3	3.0	3.1
	max.	3.7	3.5	3.7	4.0	3.4	3.5	3.3	3.5	3.5	3.6
Ecological indicator value (EIV): Nutrients	mean	3.6	3.4	3.4	3.4	2.9	3.1	3.0	3.5	3.9	3.4
	min.	3.3	3.0	2.7	2.8	2.8	3.0	3.0	3.3	3.5	3.0
	max.	4.0	3.5	4.0	4.0	3.0	3.3	3.0	3.8	4.7	3.7

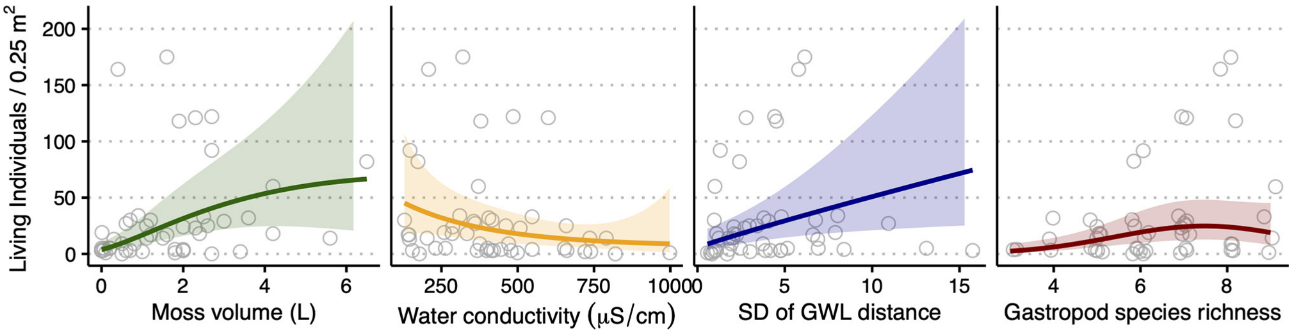

Fig. 7. The four variables influencing the abundance of living *Cochlicopa nitens* individuals at the microhabitat scale: moss volume, water conductivity, standard deviation (SD) of groundwater level (GWL) distance and the number of gastropod species. The regression lines are shown from the generalised linear mixed effect model (GLMM), the 95%-confidence intervals and the raw data points in grey

Table 3. Summary of the generalised linear mixed effect model (GLMM) for the number of living *Cochlicopa nitens* individuals

Vitality measure	Term	Estimate	SE	z	p
Living Ind. (negativ-binomial)	(Intercept)	3.063	0.348	8.810	< 0.001
	SD Groundwater level	0.533	0.187	2.857	0.004
	Moss volume linear	0.870	0.167	5.199	< 0.001
	Moss volume quadratic	−0.161	0.128	−1.256	0.209
	Water conductivity linear	−0.459	0.149	−3.074	0.002
	Water conductivity quadratic	0.054	0.137	0.395	0.693
	Mollusc species richness linear	0.393	0.143	2.738	0.006
	Mollusc species richness quadratic	−0.262	0.119	−2.210	0.027

DISCUSSION

We confirm all nine populations of *C. nitens* in Switzerland. The vitality measures varied between populations, with the ones at Lake Neuchâtel (sites no. 3–7) revealing highest vitality and the ones at the Rhine River (sites no. 8 and 9) lowest. Site no. 1 and 2 showed intermediate vitality. We report seven unknown populations at Lake Neuchâtel, resulting in a total of 16 confirmed *C. nitens* populations in Switzerland. At Lake Burgäschi, *C. nitens* most likely went extinct after the lake level was lowered by 2 m in 1943 to gain agricultural land, with a disappearance of floating mats at the lakeshore (Büren 1949) and a strong eutrophication in subsequent decades (Lachavanne 1979).

HABITAT PREFERENCE OF *COCHLICOPA NITENS* IN SWITZERLAND

The populations of *C. nitens* revealed a strong preference for open, unforested *Magnocaricion* habitats, mostly of the type *Caricetum elatae*. Sporadically, we also found low densities of *C. nitens* in *Phragmition, Molinion* or *Caricion davallianae*. In a classical zonation scheme of a lakeshore, the *Magnocaricion* lies in between the *Phragmition* (being located nearest) and the *Caricion davallianae* and *Molinion* (being located the farthest from the pelagial zone). Accordingly, groundwater levels show temporal fluctuations of about 60 cm, and short-term flooding occur frequently (Delarze et al. 2015). Whilst *Magnocaricion* appears to be the main habitat of *C. nitens*, occasional dislodgement and (temporal) colonisation of other adjacent habitats during flooding events seems probable as they are important factors influencing gastropod species richness, turnover and densities in lake- and river floodplains (Čejka et al. 2008, Ilg et al. 2009).

We could not confirm a preference for flooded forests or bushes (Cucherat & Boca 2005, Ormio et al. 2016) at the habitat scale, nor for half-shaded areas in close proximity to *Salix*-bushes at the microhabitat scale, as proposed from observations in Sweden (von Proschwitz 1998, 2006a, 2006b, 2007, 2010, unpublished data). At each site, we included the adjacent shrubs or forested areas in the search of *C. nitens*. Explanations could be (1) a regionally different habitat preference of *C. nitens*, (2) the dislodgement of individuals or shells into forested areas, or (3) the fact that many woody plants exhibit limited flooding tolerance (Glenz et al. 2006) and grow perhaps in parts of fens or wetlands that are not inundated for a too long time period. Hence an opportunistic observation of *C. nitens* rather reflects the ideal water level distance, instead of the vegetation type. Lastly (4), many of the Swedish sites are or have been heavily grazed by livestock, which seems detrimental to many gastropod species (Ausden et al. 2005, Boschi & Baur 2007a, Denmead et al. 2015). While avoiding completely wooded areas, the periphery of bushes might to some extent shelter *C. nitens* from trampling pressure of livestock.

Our results confirm the species' high demand of moisture, as attributed in previous works (von Proschwitz 1998, 2006a, 2006b, 2007, 2010, Castella et al. 2001, ArtDatabanken 2026). We underline this, with the marked preference of *C. nitens* for large moss volumes (retaining humidity, granting a stable microclimate) and a small distance to the groundwater level (optimum at around 24 cm). *C. nitens* seems to avoid both too dry and too wet sites. Ilg et al. (2011) found gastropod species and functional diversity to peak at intermediate flood disturbance and moisture levels. At both extreme ends of the hydrological gradient, only a few specialised species could survive. *C. nitens* does not seem to be one of these specialists, as high densities of *C. nitens* were also associated with a generally high gastropod species richness.

Furthermore, we found higher densities of *C. nitens* in plots characterised by a high variation in the distance to the groundwater level (micro-topography), which resulted mostly due to the prevalence of tussock forming sedges, notably *Carex elata*. Tussock forming sedges act as important ecosystem engineers structuring wetlands and influencing microhabitats (Crain & Bertness 2005, Peach & Zedler 2006). From this, we conclude that *C. nitens* requires microhabitats that allow for small-scale vertical migration during periodic increases in water levels (Plum 2005, Kotowski et al. 2013, Nicolai & Ansart 2017). A particular proneness of *C. nitens* to winter flooding events can be expected, as we found most individuals buried and inactive (with the formation of an epiphragma) in the top layers of moss and soil in November (likely to avoid freezing). However, in October we found individuals in the vegetation and resting on reed stalks approximately 30 cm above the waterline.

Water conductivity indirectly approximates the groundwater mineral richness, particularly of Ca^{2+} and Mg^{2+} ions (Horsák et al. 2014). Many gastropod species prefer intermediate levels somewhere between 300–600 µS/cm, showing unimodal relationships to the water conductivity gradient (Schenková et al. 2012, Horsák et al. 2014). We suggest that *C. nitens* is not an exception to this pattern, as the microhabitats we investigated did not show water conductivity values lower than 98 µS/cm. Considering also the measured pH-values at each site, we confirm a preference of *C. nitens* for calcareous substrate as stated before (Kerney et al. 1983, Turner et al. 1998, von Proschwitz 2006a, Rüetschi et al. 2012, Wiese 2024).

CONSERVATION OF *COCHLICOPA NITENS*

Despite the positive study results and the fact, that all sites except one are nature protected areas and therefore managed extensively and in accordance with their protection aims, we conclude a high extinction risk of *C. nitens* at the national level.

The most important aspect in the conservation of the species' populations is perhaps a natural and stable water regime (von Proschwitz 1998, 2006a, 2006b, Rüetschi et al. 2012, ArtDatabanken 2026). As our results suggest, *C. nitens* is particularly prone to more severe drought or flooding events (Nicolai & Ansart 2017), which can be expected by ongoing climate change (IPCC et al. 2022). At sites nos. 8 and 9 next to the Rhine River, the populations seem to be on the verge of extinction as all of their vitality measures were close to zero. In spring 2025, the water level of Lake Constance, one of the few unregulated prealpine lakes (Schmieder et al. 2004), reached a historic low point, falling below the 5th percentile of the 1991–2020 reference period (BAFU 2026). Consequently, the Rhine River carried little water and the habitats of *C. nitens* probably dried out for several weeks. It remains uncertain whether the populations can recover from such extreme drought events. All water bodies at the other sites are regulated and therefore less prone to such vast water level changes in the medium term. Nevertheless, extraordinary flooding events have occurred for example at Lake Neuchâtel in recent years (2015, 2021, 2023) (BAFU 2026), and more are to be expected in the future. However, implementing conservation actions restoring or improving the hydrology of wetlands is challenging (Acreman et al. 2007) and could increase the risk of too frequent or too long flooding, reducing gastropod populations in the long run (Čejka et al. 2008, Ilg et al. 2011). In Switzerland, most populations are located next to big lakes or rivers with dense infrastructure, thus improving the water regime as a conservation measure is highly unlikely. In this case, conservation actions should rather focus on site management.

All sites with populations of *C. nitens* in Switzerland are extensively managed, with partial mowing roughly once per year in late autumn or winter, depending on the accessibility of each site due to wetness. None of the sites are grazed. In pure *Phragmition* stands or in areas with strong shrub encroachment, we rarely found *C. nitens* and always in low abundances. The authors of the Swiss Red List argued, that beside drainage and destruction of wetlands, shrub encroachment / reforestation and eutrophication of water bodies are possible threats to *C. nitens* (TURNER et al. 1998, RÜETSCHI et al. 2012). This is supported by reports from Sweden (VON PROSCHWITZ 1998, 2006a, ARTDATABANKEN 2026). From this, we conclude that continuous site management is in general beneficial for *C. nitens* in secondary habitats with disrupted water regimes (which is true for all populations in Switzerland), as reed and bush encroachment pose threats to unmanaged wetlands (GÜSEWELL et al. 2000, ZEDLER & KERCHER 2004, KOŁOS & BANASZUK 2013, KOZUB et al. 2019, HÁJEK et al. 2020, HÁJKOVÁ et al. 2022).

However, the management has to take into account conflicting objectives conserving other target organism groups, including birds, plants and insects (BRÄU & NUNNER 2003, PECH et al. 2015, ANTONIAZZA et al. 2018) amongst others. Also, FARKAS et al. (2024, 2025) have shown, that mowing can reduce gastropod species richness and abundance, as individuals are removed with the cut plant biomass from the meadow. Moreover, the microclimate changes drastically after a mowing event, increasing the risk of desiccation for gastropods (BRÄU & NUNNER 2003, MARTÍNEZ-DE LEÓN et al. 2022).

MANAGEMENT RECOMMENDATIONS

We suggest the following site management for *C. nitens*: Mowing should take place late in the year, when most gastropods are buried in the soil. If possible, usage of hand-held mowers should be preferred over large tracked mowers. The latter reduce all of the important microhabitat-aspects for *C. nitens* with their caterpillar tracks, namely micro-topography, cover of tussock-forming sedges and cover of moss (KOTOWSKI et al. 2013, CEULEMANS & EMSENS 2025). As proposed by LIPIŃSKA & BIELAŃSKI (2022) raised cutting height can further protect the moss and litter layer and allow for tussock formation of sedges. Furthermore, the risk of harmful management can be reduced by leaving refugia patches uncut, where bush encroachment or reed overgrowth is limited. In rare occasions where conflicts with other conservation aims can be neglected, also mulching might be a gastropod-friendly management practice, as proposed by FARKAS et al. (2025). However, we suggest grazing is no alternative to mowing, as excessive grazing has led to multiple local extinctions of *C. nitens* in Gotland (VON PROSCHWITZ 1998, 2010, ARTDATABANKEN 2026). If mowing is not sufficient or too problematic, bush encroachment should be limited by carefully removing saplings in manual labour instead of using big, motorised machinery. Considering these recommendations, *C. nitens* populations can hopefully be preserved in the future.

Although scientific knowledge is improving (BRÄU & NUNNER 2003, BOSCHI & BAUR 2007a, 2007b, LIPIŃSKA & BIELAŃSKI 2022, MARTÍNEZ-DE LEÓN et al. 2022, FARKAS et al. 2024), our general understanding on the direct effects of site management on gastropod communities remains limited. We do not fully understand the impact of land-use intensity, management practices, timing of intervention, etc. in the long run. Our recommendations should thus be considered cautiously and adapted to site-specific conditions and trade-offs. To preserve characteristic and threatened gastropod species, future research should focus on the medium- and long-term effects of different management practices and their impact on gastropod diversity and abundance. Ideally, studies focus on the most vulnerable species for which little to no knowledge of their ecology is available, but where the need for action is high.

ACKNOWLEDGEMENTS

We thank the cantonal authorities of Bern (THOMAS LEU, JONAS LEUENBERGER) and Schaffhausen (JEANNINE KLAIBER) for supporting the study financially and in terms of content. Furthermore, we thank GEORG ARMBRUSTER, FRANÇOIS CLAUDE, EIKE NEUBERT and JÖRG RÜETSCHI for their helpful advice on the determination, distribution and ecology of *Cochlicopa nitens*. Lastly, we thank TOBIAS ROTH for his support in the statistical analyses.

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Received: February 19th, 2026
Revised: April 19th, 2026
Accepted: April 20th, 2026
Published on-line: May 22nd, 2026

APPENDIX

Table S1. Result of the generalised linear model (GLM) of the presence-absence of *Cochlicopa nitens* on the habitat scale

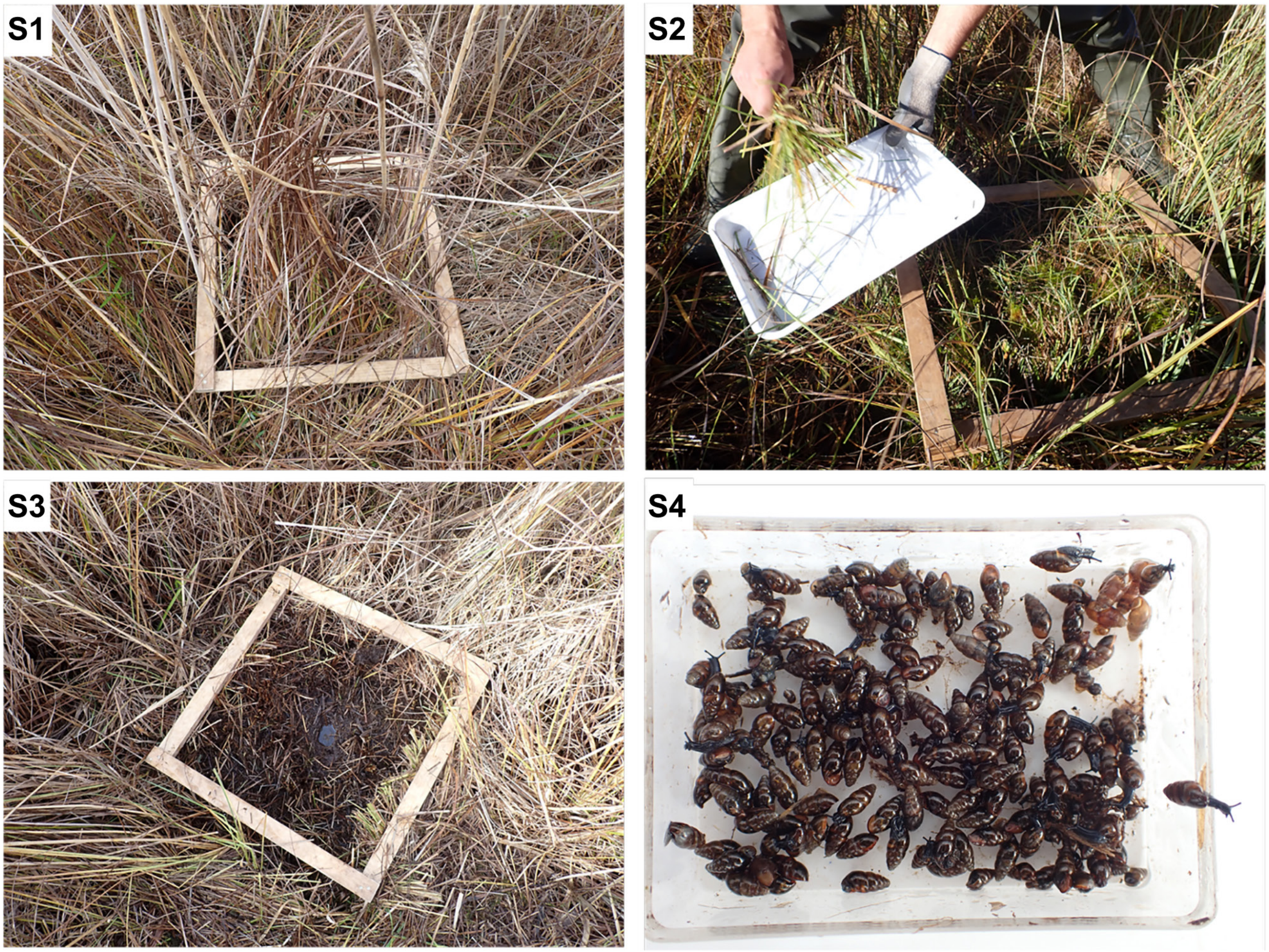
Model	Term	df	χ^2	p
Groundwater level distance and habitat type	groundwater level distance linear	1	2.99	0.084
	groundwater level distance linear quadratic	1	3.70	0.054
	habitat type (TypoCH)	3	14.86	0.002
Groundwater level distance	groundwater level distance linear	1	5.38	0.020
	groundwater level distance linear quadratic	1	10.15	0.001
	site	2	0.18	0.914

Table S2. Frequency of the gastropod species present in the n = 53 plots of *Cochlicopa nitens* at the microhabitat scale

Name	Frequency (abs.)	Frequency (rel.)
Vertigo antivertigo	49	92.5
Euconulus alderi	43	81.1
Zonitoides nitidus	39	73.6
Deroceras laeve	34	64.2
Vertigo moulinsiana	34	64.2
Succinea putris	33	62.3
Trochulus sericeus	19	35.8
Cochlicopa lubrica	17	32.1
Carychium spp.	15	28.3
Vitrinobrachium breve	11	20.8
Galba truncatula	7	13.2
Vallonia pulchella	6	11.3
Fruticicola fruticum	5	9.4
Punctum pygmaeum	4	7.5
Bithynia tentaculata	3	5.7
Cepaea nemoralis	3	5.7
Perforatella incarnata	2	3.8
Planorbis planorbis	2	3.8
Vertigo pygmaea	2	3.8
Vertigo substriata	2	3.8
Columella edentula	1	1.9
Hygromia cinctella	1	1.9
Planorbarius corneus	1	1.9
Segmentina nitida	1	1.9

Table S3. Frequency of the vascular plant species present in the n = 53 plots of *Cochlicopa nitens* at the microhabitat scale

Name	Frequency (abs.)	Frequency (rel.)
Phragmites australis	50	94.3
Carex elata	44	83.0
Galium palustre	15	28.3
Mentha aquatica	13	24.5
Carex acutiformis	5	9.4
Agrostis spp.	4	7.5
Hydrocotyle vulgaris	4	7.5
Symphytum officinale	4	7.5
Typha latifolia	4	7.5
Carex appropinquata	3	5.7
Carex flacca	3	5.7
Carex riparia	3	5.7
Cladium mariscus	3	5.7
Filipendula ulmaria	3	5.7
Thalictrum flavum	3	5.7
Epilobium spp.	2	3.8
Juncus effusus	2	3.8
Juncus subnodulosus	2	3.8
Lathyrus palustris	2	3.8
Lotus pedunculatus	2	3.8
Lysimachia vulgaris	2	3.8
Solidago gigantea	2	3.8
Thelypteris palustris	2	3.8
Typha angustifolia	2	3.8
Typha spp.	2	3.8
Calamagrostis spp.	1	1.9
Carex spp.	1	1.9
Equisetum palustre	1	1.9
Galium aparine	1	1.9
Hypericum tetrapterum	1	1.9
Juncus spp.	1	1.9
Medicago lupulina	1	1.9
Molinia caerulea	1	1.9
Ranunculus repens	1	1.9
Schoenus ferrugineus	1	1.9
Senecio paludosa	1	1.9
Stachys palustris	1	1.9
Urtica dioica	1	1.9
Valeriana officinalis	1	1.9



Figs S1–4. Sampling of *Cochlicopa nitens* at the microhabitat scale: 1 – plot of 0.25 m^2 in *Magnocaricion* vegetation before removal of the vegetation; 2 – the vegetation is cut, beaten over a white plate (detaching climbing individuals) and removed from the plot; 3 – plot after removal of vegetation including moss and litter layer; 4 – the collected and counted *C. nitens* individuals