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Ecology and Current Distribution of Three Habitat-specialized Land Snail Species of the Genus *Vertigo* (Gastropoda: Eupulmonata) in Europe

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Our understanding of the species distribution and ecology is critical to properly assess its conservation status. *Vertigo lilljeborgi*, *V. genesii*, and *V. geyeri* have the center of their current distribution range in northern Europe, where their occurrence is relatively frequent. However, to the south their occurrence is fragmented and restricted to sites of late glacial/early Holocene origin. In the last ~30 years, there has been an increase in records, connected with the listing of the latter two species in Annex II of the EU Habitats Directive (94/43/EEC). However, there is no comprehensive publication documenting their pan-European distribution. Therefore, we assembled all available data from online databases, books, and scientific literature and combined them with our unpublished records to create distribution maps. The results show a more frequent occurrence in temperate Europe than previously known, especially for *V. geyeri*. Analyses performed on data from 327 ecologically potentially suitable sites, covering the entire distribution range of the species, have improved our knowledge of the species ecology. *Vertigo lilljeborgi* and especially *V. genesii* are restricted to areas with lower summer and winter temperatures, therefore, their further decline is expected in the face of rising temperatures due to climate change. The preference of *V. geyeri* for higher temperatures, in comparison to the latter two species, may explain its relatively frequent distribution in temperate Europe. *Vertigo lilljeborgi* favors base-poor sites, while *V. genesii* and *V. geyeri* prefer calcium-rich sites, with the latter being the most calcicolous. Their need for a stable water regime and low-productive sites, known from previous studies, was not conspicuous in our results, in all probability due to the selection of sites well within the species range. Despite the increase in record frequency, these species are still endangered, especially in temperate Europe. Their sites should therefore be strictly protected as sites of high biological diversity and conservation value. Because of their relict nature, these land snails should be considered umbrella species and indicators of well-preserved groundwater-dependent ecosystems in temperate Europe.

Key words: Glacial relicts, Habitat specialists, EU Habitats Directive, IUCN Red List species, Climate change

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BACKGROUND

The land snails of the genus *Vertigo* O. F. Müller, 1774 are currently represented by ~100 species and subspecies (Nekola et al. 2018). They have worldwide distribution (Nekola and Coles 2016) with the majority of known species occurring in the Holarctic region and occupying variety of habitats from forests to open wetlands. Nowadays, the genus reaches its highest species richness in North America (Nekola and Coles 2010) whereas in Europe, only 15 extant species are known (von Proschwitz 2003). The affinity of several genus representatives to cold and damp habitats is most apparent in species considered glacial relics, *e.g.*, *Vertigo lilljeborgi*, *V. genesii*, and *V. geyeri* due to their wide distribution in periglacial Europe during the Late Glacial and Early Holocene (*e.g.*, Jaeckel 1962; Ložek 1964; Ložek 1992). They are currently restricted to wetland habitats, predominantly to minerotrophic fens (Cameron et al. 2003; Schenková and Horsák 2013a). With the climate change at the end of the last glacial, their main distribution area shifted to the boreal and arctic zones. In the temperate zone, however, they settled in the middle and more often in the higher elevations of the main mountain systems. As these occurrences are rare and fragmentary, the two former species have been listed in Annex II of the EU Habitats Directive (92/43/EHS). The presence of *V. geyeri* has been shown to indicate ancient origin of particular sites with the age spanning from hundreds to thousands of years (Hájek et al. 2011; Horsák et al. 2012; Peterka et al. 2021), making it a valuable umbrella species. For the other two species, relict status is also expected (Schenková and Horsák 2013a; Horsák et al. 2017). All three species are mainly threatened by human impacts, namely by direct destruction of habitats, drainage, and nutrient input followed by succession towards more productive habitats that cannot support their persistence (*e.g.*, Cameron et al. 2003; Vavrová et al. 2009; Horsák et al. 2017; Horsáková et al. 2018). They are also very likely to be threatened by climate change due its impact on the site hydrology (Essl et al. 2012; Gong et al. 2012; Coufal et al. 2023). Until recently, the knowledge on distribution of these species in temperate Europe was substantially underestimated as malacologists have mostly focused on different types of habitats. For example, *V. geyeri* was found in Czechia for the first time in 1991 (Ložek 1993). However, this single known population became extinct due to inadequate conservation management of the site. After that, the species was considered extinct in the country until another population was discovered in 2011 (Myšák et al. 2012), followed by two dozen of newly discovered sites (*e.g.*, Schenková and Horsák 2013b; Coufal 2019). Not only in Czechia, but also in other European countries, the number of records of these glacial relics continues to increase due to extensive surveys and growing knowledge of the species habitats (*e.g.*, Schenková et al. 2012; Skujienė et al. 2019; Gabriel 2020). During the last three decades, many new sites of these species were discovered throughout the Europe. However, there is no outright source of the species distribution since most of the results are scattered across databases, local literature, and survey reports, making it difficult to access. On top of that, many of these findings have not been published. Furthermore, ecological demands were analyzed only for *V. lilljeborgi* (Horsák et al. 2017) and *V. geyeri* (Horsák and Hájek 2005; Schenková et al. 2012), but still based on data from a limited portion of their distribution range. These studies show that the species differ in their tolerance to water pH and air temperature. While *V. lilljeborgi* is limited to sites of neutral to slightly acidic pH (Pokryszko 1990), *V. genesii* inhabits mainly highly alkaline treeless fens (Killeen 2003). *Vertigo geyeri* is reported to have a relatively high tolerance to mineral richness variation, avoiding only extremely calcareous and very acidic mires (Cameron et al. 2003; Schenková et al. 2012). *Vertigo lilljeborgi* and *V. genesii* are predominantly restricted to areas of cold climate (Cameron et al. 2003; Horsák et al. 2017), while *V. geyeri* is commonly found also in warmer areas (Schenková et al. 2012).

The current increase in distributional data about these three wetland specialists calls for: 1) assembling as many unpublished records on their occurrence as possible, 2) creating maps of their currently known distribution in Europe based on unpublished personal records in combination with literature and online databases, and 3) analyzing the species ecological requirements using data spanning across their entire European distribution range.

MATERIALS AND METHODS

Study area

The studied area in this article is limited to Europe.

Quantitative sampling (personal records)

Sites selected for sampling covered only minerotrophic fens as these are the main habitats supporting persistence of the species. To sample molluscs at each surveyed site, 12 L volume sample of an upper herbaceous layer consisting of vascular plants and bryophytes was processed using wet sieving technique (for details see Horsák 2003). Dried mollusc samples were sorted and identified to the species level. Nomenclature follows Nekola et al. (2018).

Dataset for ecological analyses and environmental predictors

From all quantitatively sampled fens, we selected only sites with the occurrence of at least one of the target species. The reason for this was to conduct the analysis based on data that include also sites where the given species is absent, but at least one of the other two species is present. Therefore, all of the included sites are well preserved and of historical continuity, as they harbor at least one of these relict species. This setting ensured suitable ecological conditions and eliminated the possibility of disrupted historical continuity of the site. In total, the dataset included 103 populations of *V. lilljeborgi*, 59 of *V. genesii* and 222 of *V. geyeri* (some of them harboring two or all three of these species). The selection of environmental predictors was based on publications investigating their ecological requirements (*e.g.*, Kerney et al. 1983; Cameron et al. 2003; Horsák et al. 2017). To analyze climatic tolerance, selected air temperature variables (BIO5 = maximum temperature of warmest month, hereafter summer temperature, and BIO6 = minimum temperature of coldest month, hereafter winter temperature) were extracted using the WorldClim v1.4 database (Hijmans et al. 2005) and the ArcGIS 10.3 software. In the previous works, altitude was often found an important predictor determining the occurrence of the target species (*e.g.*, Kerney et al. 1983;

von Proschwitz 2003), especially in temperate Europe. However, the availability of direct climate data allowed us to replace altitude with ecologically more relevant climatic variables, namely air temperature.

As calcium content is an important driver of land snail distribution, water conductivity was measured during the fieldwork in waterlogged parts using digital portable device HACH HQ40d. It was found to be an excellent proxy for dissolved calcium concentration as it reflects mainly the concentration of Ca^{2+} and Mg^{2+} in fens (Horsák 2006). Because all study species strongly respond to water regime and vegetation productivity, we used Ellenberg-type indicator values (EIVs) as a proxy for site moisture and macro-nutrient availability of the studied sites. For moisture, EIVs for European species of vascular plants and bryophytes occuring in mires were used (Hájek et al. 2020). For nutrients, original Ellenberg indicator values available for vascular plants were used (Ellenberg and Leuschner 2010).

Statistical analyses

Kruskall-Wallis Rank Sum Test and Dunn post-hoc test were used to test differences among species in variation of enviromental parameters (package "FSA", Ogle et al. 2023). Prior to subsequent analyses, variables were squareroot- or log-transformed to normalize their distribution. To determine the order of environmental variable importance for each species, a classification tree (CART; Breiman et al. 1984) was computed using "rpart" package (Therneau et al. 2022). This method is used to reveal non-linear relationships between predictors. We used complexity parameter (cp) based on the tree complexity and sum of errors to determine the optimal size of the tree (number of splits). The sites with measured enviromental variables for all three species were combined and sorted into three categories for each species individually: absent, species was not recorded; weak, number of recorded live individuals per 12 L volume sample varied between 1–5 (*V. lilljeborgi*), 1–15 (*V. genesii*), and 1–10 (*V. geyeri*); strong, number of recorded live individuals varied between 6–32 (*V. lilljeborgi*), 16–157 (*V. genesii*), and 11–114 (*V. geyeri*). These numbers were chosen arbitrarily, but the rationale was to consider differences in population densities among species and to evenly divide the sites with the species presence into two equal parts. Generalized Linear Models (GLMs) were used to test the relationship between environmental predictors and presence/absence of the species on the site (binomial data). Generalized Additive Models (GAMs) were used to project relationships between species abundance and environmental predictors in cases of non-linear responses. The amount of explained variation, i.e. deviance explained, for GAMs was computed using "mgcv" package (Wood 2022). R software version 4.2.2 (R Core Team 2022) was used to compute all analyses. All graphical outputs, except classification tree, were generated using package “ggplot2” (Wickham 2016). Species distribution maps were created using the ArcGIS 10.3 software.

RESULTS

Distribution

Based on all assembled records, *Vertigo lilljeborgi* occurrs frequently in Fennoscandia and northern parts of the United Kingdom. The species was originally known from seven countries prior to 2000, while the current number has increased to 16 (Table 1). The new records are consitent with the distribution known from the older literature and show a previously unknown scattered occurrence in the Baltic states and Belarus, followed by a distribution gap spanning over Baltic Russia and Poland (Fig. 1). A relatively frequent but regionally restricted distribution was discovered in Central Europe in Czechia and adjacent parts of Germany, and a rare distribution was found in the Alps, Massif Central (France), and Pyrenees (France and Spain). The main distribution area of *V. genesii* spans over the central part of Scandinavia with scattered distribution in Finland and disjunct populations in central Alps. The new records are consitent with the *a priori* known distribution range and show a scattered distribution in southern Scandinavia, the United Kingdom and Finland, and extend previously known distribution in the Alps, with two isolated records from Austria and Spain (Fig. 2). The species was known from six countries prior to 2000, while now the number has increased to ten (Table 1). The new records of *V. geyeri* confirm the previously reported main area of distribution in Scandinavia and discontinuous populations in Finland and the Alps. Nevertheless, a plethora of sites was discovered in the Baltic states, Belarus, Poland, Slovakia, Czechia and the Alps, with the southeasternmost records from the Romanian Carpathians and the southernmost from the Apennine Mountains (Fig. 3). The species was formerly known from ten countries, while to date the extant populations have been documented from 20 countries (Table 1). Most of the records of *V. genesii* and *V. geyeri* come from around and after 2000, while the records of *V. lilljeborgi* are more evenly distributed over time (Fig. 4). Unpublished records of all species are summarized in table S1.

Table 1. Species distribution in countries. Symbols: † - extinct; ? – dubious records; * - rare (1-9 sites); ** - scattered (10-29 sites); (***) - frequent only locally or regionally (30 and more sites); *** - widespread (30 and more sites); grey, occurrence known prior to 2003 (Kerney et al. 1983; Cameron et al. 2003). Frequency is based on actual records, not literature estimates

Country	Species		
	V. lilljeborgi	*V. genesii*	*V. geyeri*
Norway	***	**	**
Finland	***	**	**
Sweden	***	(***)	***
Estonia	*	?	**
Latvia	**	?	*
Lithuania	*	?	(**)
Denmark	*	-	***
Belarus	*	-	**
Ireland	***	**	***
Great Britain	***	***	***
Germany	*	-	**
Poland	-	-	***
Ukraine	-	-	†
France	**	*	(***)
Czechia	**	-	(***)
Slovakia	-	-	(***)
Switzerland	*	***	(***)
Austria	*	*	**
Romania	-	-	*
Slovenia	-	-	-
Italy	-	*	*
Spain	*	*	-

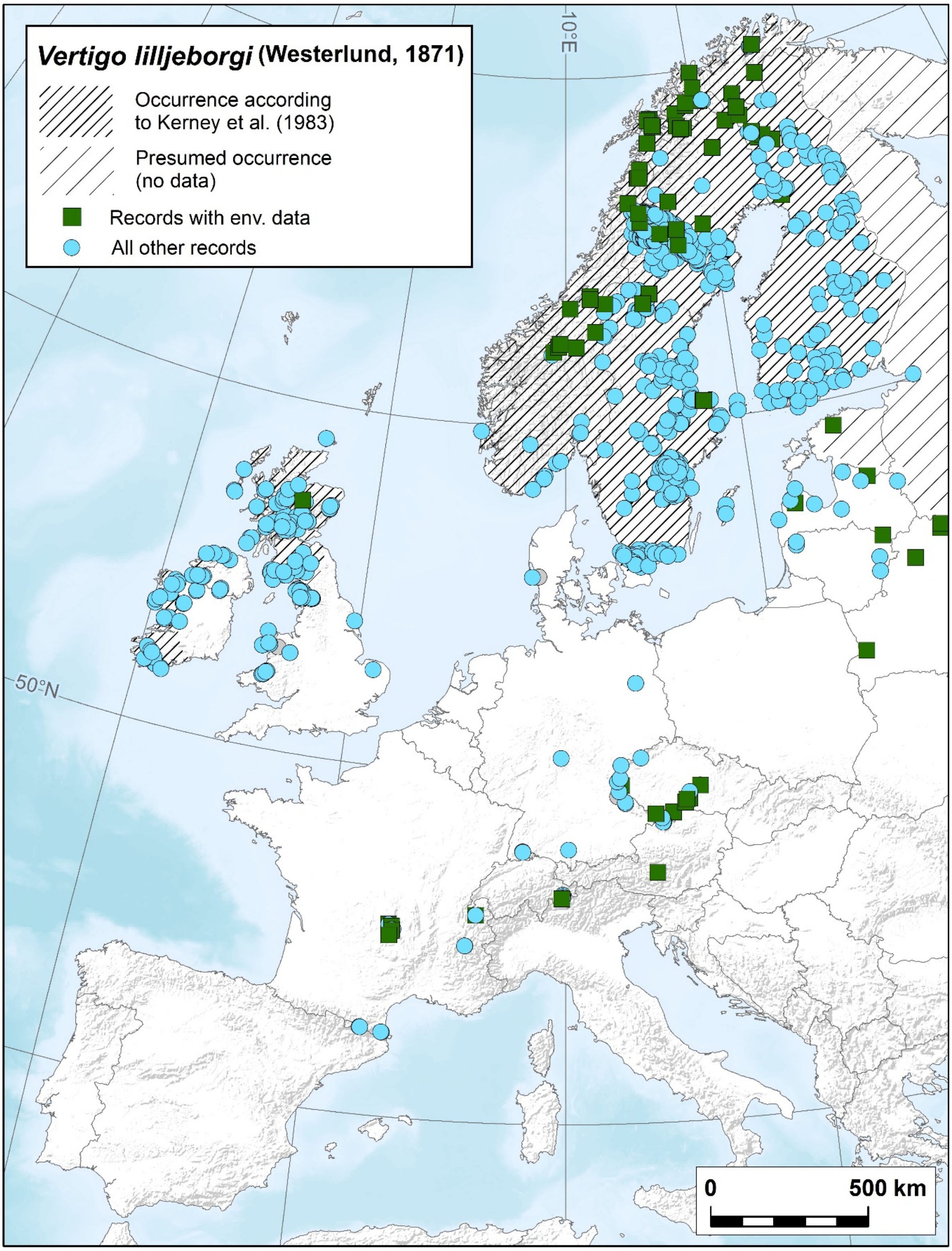

Fig. 1. *Vertigo lilljeborgi* distribution map.

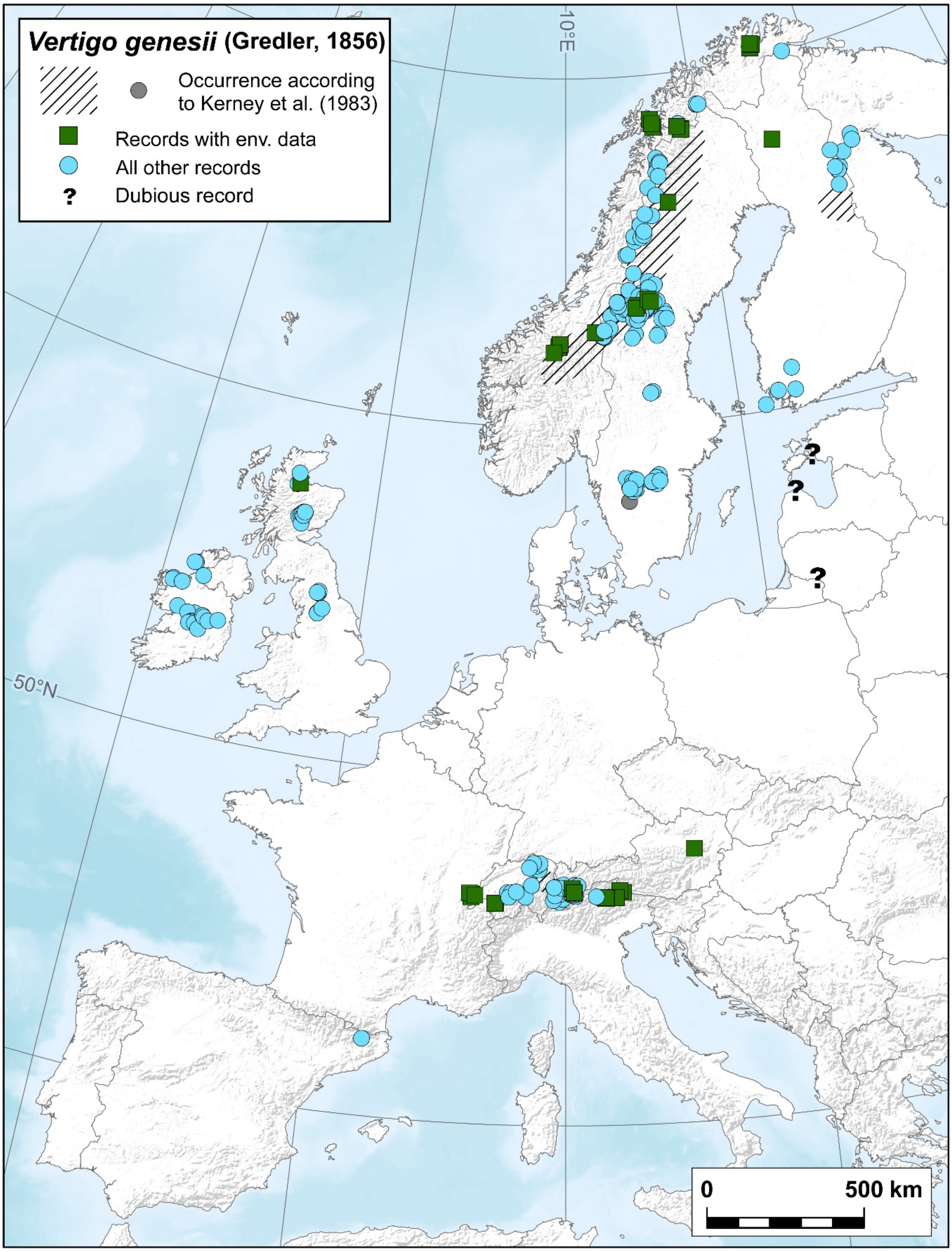

Fig. 2. *Vertigo genesii* distribution map.

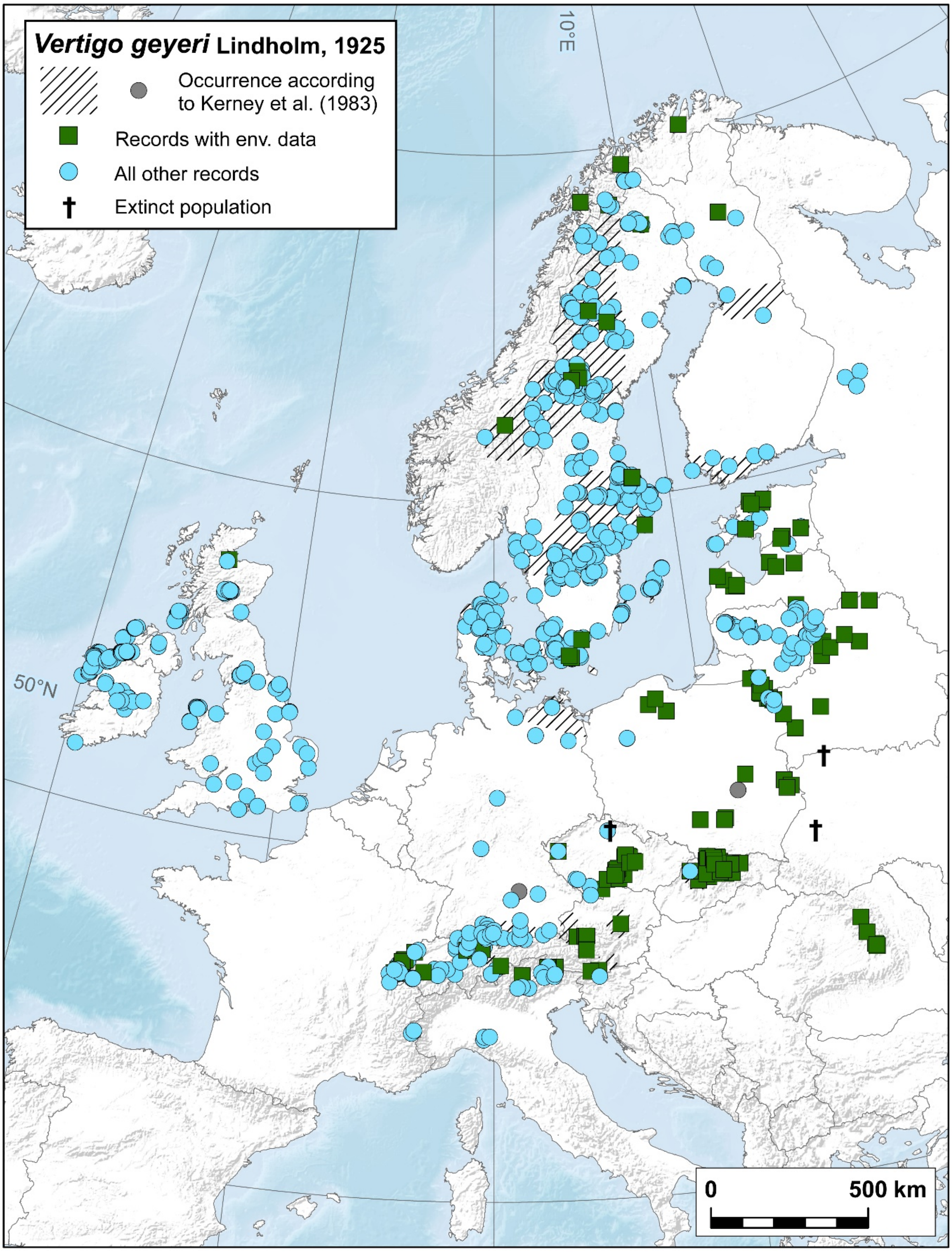

Fig. 3. *Vertigo geyeri* distribution map.

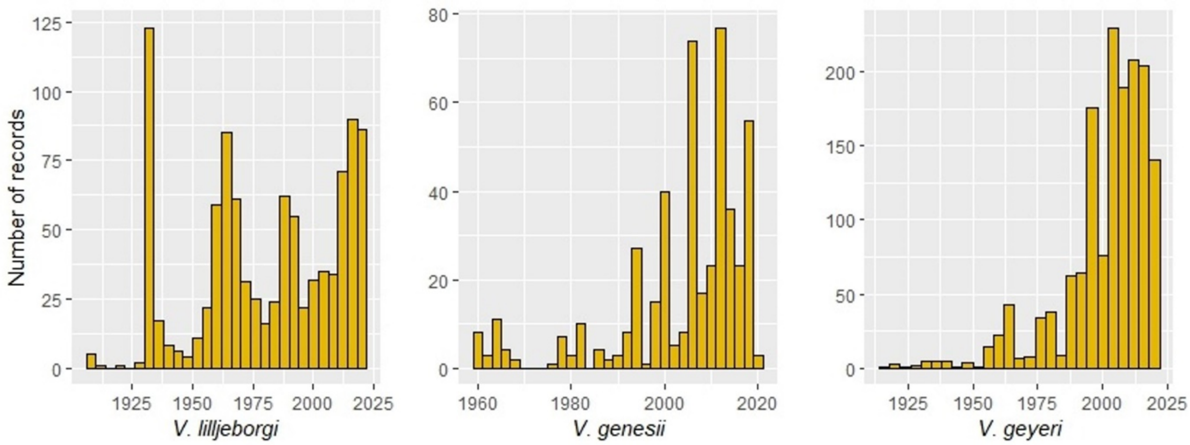

Fig. 4. Histograms showing frequency of all assembled records over time.

Ecological requirements

Based on available data we found that *Vertigo lilljeborgi* occupies a relatively broad temperature range but has a narrow alkalinity niche that restricts it to mineral-poorer sites (Fig. 5). Accordingly, the classification tree showed that it prefers sites with low alkalinity, lower summer temperatures, high waterlogging, and avoids extremely oligotrophic conditions, *i.e.*, sites with water conductivity below 224 µS/cm, July temperatures below 20°C, moisture above 8 EIV, and nutrient availability above 2.1 EIV (Fig. 6a; Table 2). In concordance, the Generalized Linear Models (GLMs; Table 3; Fig. S1) showed that *V. lilljeborgi* occurrs mainly at sites with lower summer and winter temperature, low alkalinity and high moisture. The species showed a unimodal response to summer temperature as its abundace peaked around 17°C (Dev. Explained: 0.16; $p < 0.001$; Fig. 7). *Vertigo genesii* avoids sites of high summer temperature, and prefers rather alkaline and low productive sites (Fig. 5). Similarly, the classification tree analysis showed its affinity for colder climate and higher water conductivity, *i.e.*, summer temperatures below 16°C and water conductivity above 137 µS/cm (Fig. 6b; Table 2). Likewise, GLMs supported its preference for lower summer and winter temperatures (Table 3; Fig. S1).

Table 2. Percentages of variation explained by environmental predictors in classification tree

Predictor	Predictor importance (%)		
	V. lilljeborgi	*V. genesii*	*V. geyeri*
T in warmest month	22	**50**	**37**
T in coldest month	14	4	26
Water conductivity	**33**	29	13
Moisture	11	10	4
Nutrients	14	4	12
Total explained variation	35	63	52

Table 3. Results of Generalized Linear Models (GAMs) on binary data (presence/absence) showing preferred niche with regard to analysed predictors. Preferred niche is considered the span from presence (1) to the middle range (0.5) in comparison to values under middle range to absence (below 0.5). Only significant results with explained variation ≥ 0.10 are shown. For details see figure S1

	Preferred niche					
Predictor	*V. lilljeborgi*	Adj. R^2	*V. genesii*	Adj. R^2	*V. geyeri*	Adj. R^2
T in warmest month (°C)	12.5–17.5	0.15***	12.5–15.9	0.35***	18–25°C	0.41***
T in coldest month (°C)	22–12	0.17***	(-19)–(-2.5)	0.10***	(-9.5)–(-2.0)	0.12***
Water conductivity (μS/cm)	21–160	0.15***	-	n. s.	140–950	0.15***
Moisture (EIV)	8.4–9	0.11***	-	n. s.	2.3–3.9	0.10***
Nutrients (EIV)	-	n. s.	-	n. s.	-	n. s.

Vertigo geyeri showed an affinity for sites with warmer temperatures (summer and winter) and a broad niche with respect to water conductivity and nutrient availability, with these predictors having the highest median values of all species (Fig. 5). The classification tree showed an affinity for warmer sites with higher alkalinity and lower nutrient availability. Specifically, sites with summer temperatures above 18.5°C and winter temperatures above 12°C, with water conductivity above 359 μS/cm, and nutrient availability below 2.7 EIV (Fig. 6c; Table 2). Similarly, GLMs showed preferrence for higher summer and winter temperatures, and a tolerance to a large variation in water conductivity. Nevertheless, GLMs showed a rather wide tolerance to nutrient availability (Table 3; Fig. S1). The abundance of the species increased with increasing summer temperature up to 21°C and then reached a pleateau (Dev. Explained: 0.26; $p < 0.001$; GAMs; Fig. 8) and increased in response to increasing water conductivity, peaking at 550 μS/cm and then decreasing (Dev. Explained: 0.14; $p < 0.001$).

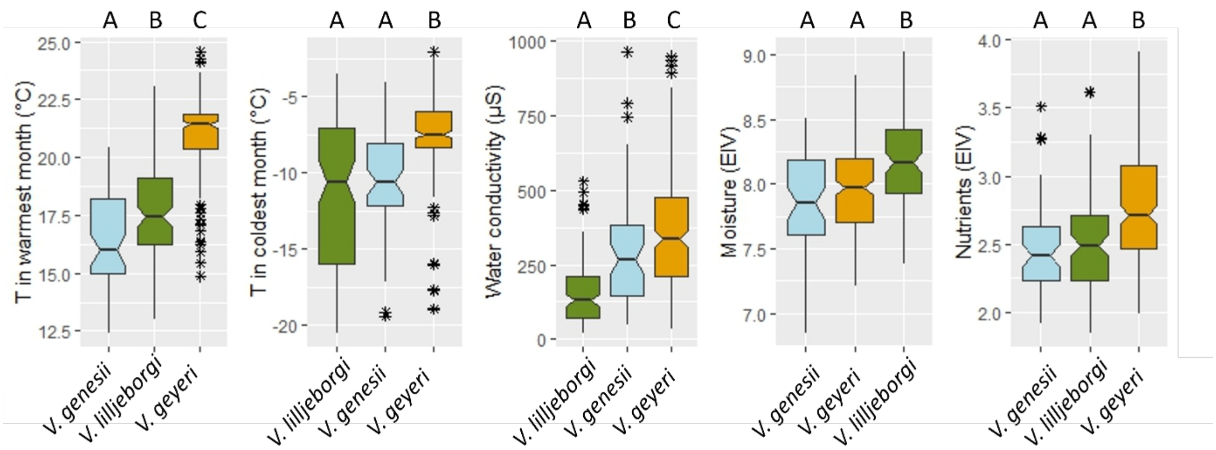

Fig. 5. Variation of analysed environmental predictors using box and whisker plots. Letters above boxplots indicate homogeneous/heterogeneous groups (Kruskal-Wallis test followed by Dunn post hoc text). The central line of each boxplot refers to the median value, box indicates the first and third quartile, whiskers refer to the non-outlier values and asterisks indicate outliers.

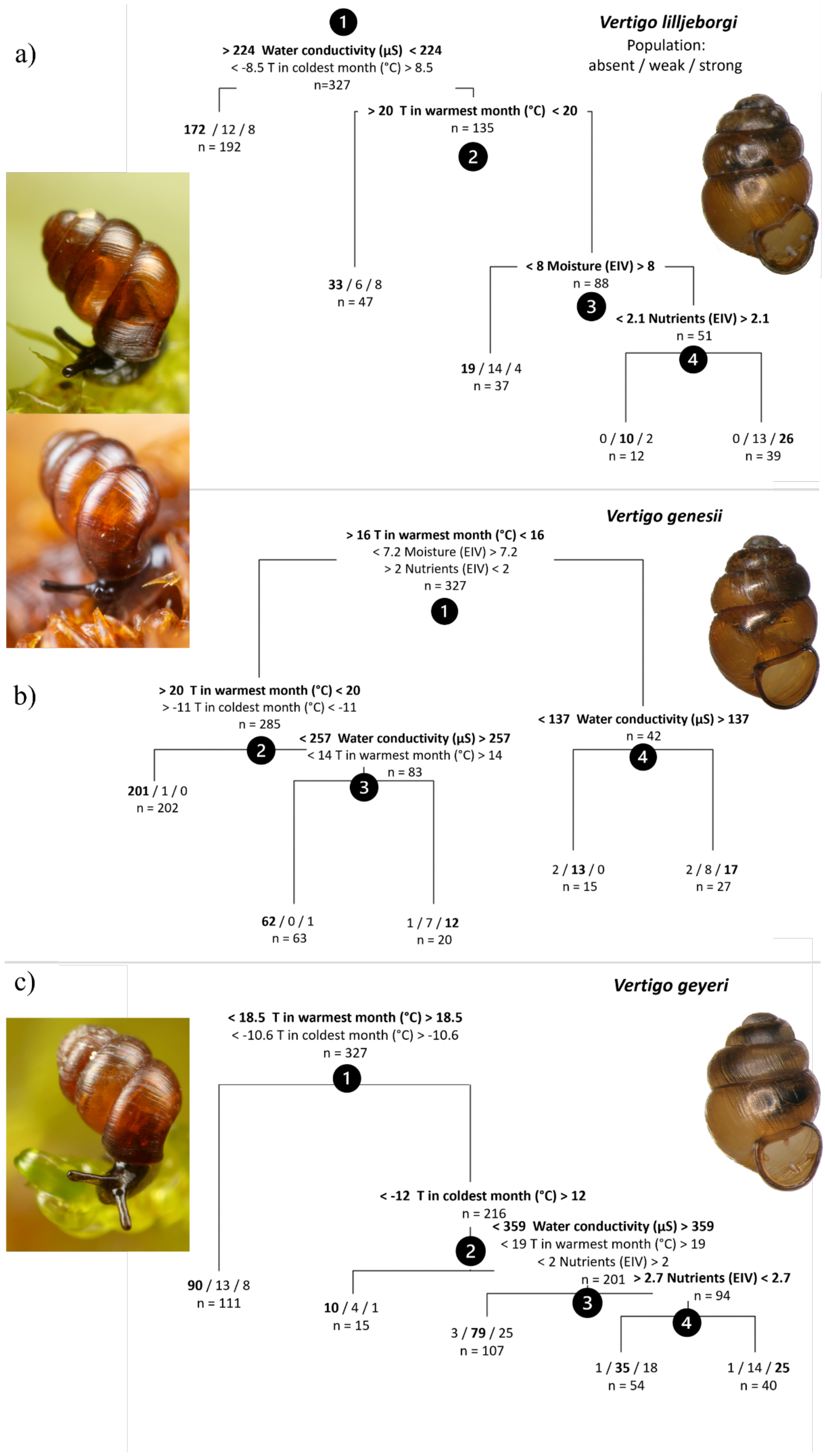

Fig. 6. Classification tree for the occurrence of a) *V. lilljeborgi*, b) *V. genesii* and c) *V. geyeri* at 327 sites. Numbers at each node indicate that the species was: absent/low population density/high population density,

respectively. See Materials and Methods for details. The major splitter predictor and its split values are in bold whereas surrogates (i.e. predictors that distribute at least 90% of the cases to the same group as the primary splitter) are below the major splitter. Numbers in black circles indicate number of splits. Photographs: Radovan Coufal (live individuals), Michal Horsák (shells).

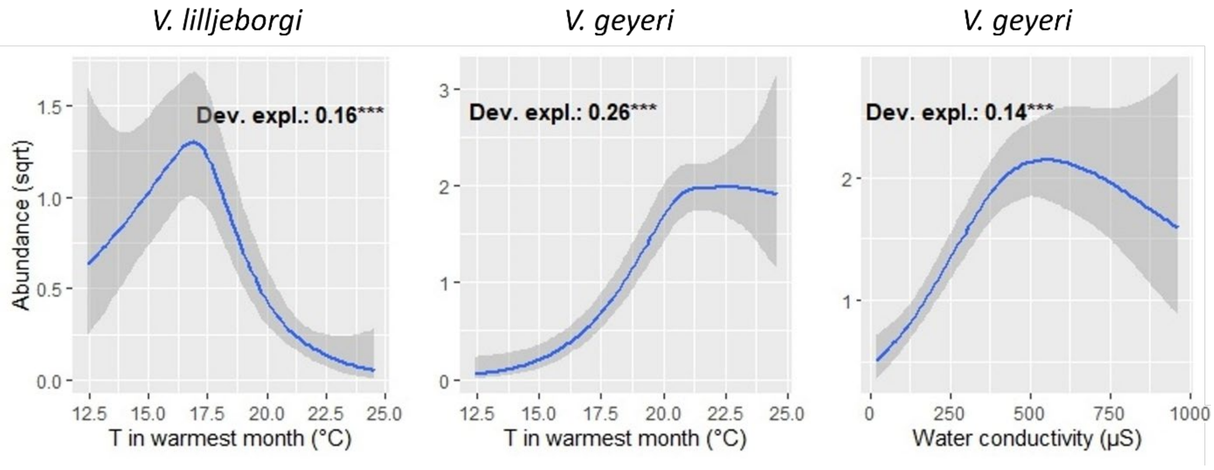

Fig. 7. Generalized Additive Models (GAMs) showing relationships between square rooted abundance of the species and explanatory variable. Only significant relationships with unimodal distribution are shown. Abbreviation: Dev. expl., Deviance explained, *i.e.*, a variable showing variance explained by GAMs. Shaded stripes indicate 95% confidence interval.

DISCUSSION

Vertigo lilljeborgi

Distribution

The main distribution area of *Vertigo lilljeborgi* spans over the boreal and arctic zones (see von Proschwitz 1993 2003; von Proschwitz et al. 2023). It has the most continuous occurrence in Fennoscandia when compared to the other two species and is also frequent in the northwestern parts of Great Britain and Ireland. Regarding these regions, the new records confirm the distribution documented by Kerney et al. (1983), with the exception of the southern half of Great Britain where new sites have been discovered. The new personal records presented here show relatively rare and scattered occurrence in Lithuania, Latvia and Belarus as expected by Schenková and Horsák (2013a). Only one site is known from Estonia (data presented here), however, this region is underexplored and the species is likely to be more widespread there, as the records from adjacent countries suggest. The Baltic States region represents a transition zone between the frequent occurrence in Fennoscandia and the rare occurrence southwards, *i.e.*, south of the area where the Scandinavian ice sheet occurred during the Last Glacial Maximum (LGM; Hughes et al. 2013). Poland and the Western Carpathians represent malacologically well explored regions with many ecologically suitable sites (*e.g.*, Horsák and Hájek 2003; Schenková et al. 2012). Nevertheless, the species seems to be absent there, probably due to dispersal limitations (Horsák et al. 2017). The main area of distribution in temperate Europe appears to be in the Bohemian Massif in Czechia and adjacent locations in Germany (data presented here; Schenková and Horsák 2013a; Horsák et al. 2017; Gabriel 2020; Čejka et al. 2020). In Czechia, most of the sites are severely damaged by human impact and the species occurrs there in low abundances, likely living on extinction debt (pers. obs.; see Discussion in Horsák et al. 2017). Despite the extensive sampling and numerous ecologically suitable sites, *V. lilljeborgi* is very rare in the Alps. In Austria, only one site is known (data presented here) while there are five sites in the Swiss and French Alps (Turner et al. 1998; Schenková and Horsák 2013a; Combrisson and Vuinée 2017). This supports its relictual status as the species was likely influenced more by extinction than colonisation events (Horsák et al. 2017). The known occurrence in France includes sites in the Massif Central and Western Alps (Vrignaud 2012; Lecaplain 2013; Horsák et al. 2017) while older records from the French and Spanish Pyrenees mark the known southern edge of distribution (van Regteren Altena 1934; von Proschwitz 2004). However, the minerotrophic fens of the Pyrenees and the Cantabrian Mountains are malacologically very poorly explored, therefore, the species may be more common there due to the presence of ecologically suitable sites (Jiménez-Alfaro et al. 2014).

Ecology

According to the literature, the species inhabits mires, marshy lake margins with *Carex* vegetation and marshes with slightly acidic to neutral pH, low to intermediate alkalinity and high water table (Kerney et al. 1983; von Proschwitz 1993 2003; Schenková and Horsák 2013a; Nekola et al. 2018). Correspondingly, Horsák et al. (2017) showed on data from relic sites of temperate Europe and southern Scandinavia that the species inhabits predominantly strongly waterlogged slightly acidic to neutral sites with higher vegetation productivity. This is consistent with our results which showed that the species prefers the most waterlogged and base-poor sites of all analysed species. Accordingly, von Proschwitz (1993) showed that the species optimum in Sweden is at neutral sites with a pH value around 6.1. The response of abundance to summer temperature is unimodal, however, while Horsák et al. (2017) showed the peak around 14°C, our data show a peak around 17°C. This is surprising considering that our dataset contains more sites from colder Fennoscandia. In addition, in our extended dataset the species appears to tolerate a relatively wide range of winter temperature while it preferred rather colder sites. Together with similar results from Sweden (von Proschwitz 2003), this suggests that the species is adapted for harsher conditions of continental climate.The ecological demands of northern and temperate populations were compared, however, no significant differences were found (data not shown). On the contrary, Horsák et al. (2017), analysing the differences between the boreal and temperate occurrences in terms of vegetation composition, found the boreal sites to be wetter with less productive vegetation, while temperate European sites were more acidic and productive. As we did not have vegetation composition data for all sites, we could not perform similar analyses.

Vertigo genesii

Distribution

Similarly to the previous species, the distribution of *V. genesii* was originally known mainly from the Scandinavian mountain ranges, Finland, and Switzerland (Kerney et al. 1983; von Proschwitz 2003; von Proschwitz et al. 2023). With the inclusion of the species into Annex II of the EU Habitats Directive (92/43/EEC), the increased survey effort led to discoveries of new sites. The majority of new records comes from Sweden, Norway, and Finland (data presented here; GBIF.org), where they extend the originally known distribution range. It is expected that the number of records will further increase in Fennoscandia, especially in northern Norway and Finland where unsurveyed suitable sites are present. Several new sites were documented also in central Ireland and the northern half of Great Britain and Ireland (Killeen et al. 2019; Conchological Society of Great Britain & Ireland 2020). Southwards from its occurrence in the southern parts of Sweden and Finland there is a large distribution gap extending to the Alps. Areas in this gap, *i.e.*, the Baltic States, northeastern Poland and Western Carpathians, the latter of ancient origin (Hájek et al. 2011; Horsák et al. 2012) represent malacologically well explored regions. However, even extensive sampling (see Schenková et al. 2012) failed to detect presence of the species. As for the previous species, this is likely due to limited dispersal ability and/or extinction events prevailing over colonisation. The knowledge on distribution range in the Swiss and Italian Alps has also been expanded (data presented herein; Turner et al. 1998; Schenková and Horsák 2013a). Despite a high sampling effort on ecologically suitable sites in Austria, *V. genesii* is only known from a single site (Duda 2015). Similarly, extensive sampling (see Lasne et al. 2021) yielded only three sites in eastern France (Jura Mountains; data presented here; Brugel 2016; Lasne 2018). The southernmost record comes from Núria near Girona, Spain (Bech 1992). The author formerly published the record as *V.* cf. *genesii*, however, the revision of the material proved the identification to be correct (Cadevall and Orozco 2016; Cadevall et al. 2020). The presence of calcareous fens in the area (*e.g.*, Jiménez-Alfaro et al. 2014) suggests that the species may occur at other localities, however, no extensive malacological survey of spring fens has been conducted in this area. Findings of juveniles or individuals of other *Vertigo* species with poorly developed aperture and dentition had led to many misidentifications and erroneous occurrence reports. Kuznecova and Skujienė (2011 2012) reported the presence of the species in Lithuania, however, in both cases juvenile individuals of other *Vertigo* species were misidentified for *V. genesii*. Pilāte (2000) reported two fossil and one subfossil individuals from Slītere National Park, Latvia. However, the description of the habitat suggests that this was likely also a misidentification. Similarly, in the report of Šatkauskienė (2001) from Lithuania, the author herself expresses doubts about the identification and mentions that more shells would be necessary to correctly identify the species. Stalažs and Dreijers (2016) state the presence of the species in all Baltic States, referring to Krausp (1940). However, prior to 1966, *V. geyeri* and *V. genesii* were not treated as separate species (Waldén 1966), therefore these records most likely refer to the closely related *V. geyeri*. The last report of occurrence comes from Spuņģis et al. (2021) from Latvia who report presence of the species based on one subfossil shell, however, this was most likely also a misidentification. Despite the extensive survey of ecologically suitable sites in the Baltic States, there are no reliable records so far. Similarly, *V. genesii* was reported also from Poland and Germany, nevertheless, these records were also based on misidentification (Cameron et al. 2003).

Ecology

According to the literature, *V. genesii* is a stenotopic species with an arctic-alpine distribution restricted to calcium-rich wetlands or wet flushes that are permanently wet but not flooded (Kerney et al. 1983; Cameron et al. 2003; Valovirta 2003; von Proschwitz 2003; Nekola et al. 2018; von Proschwitz et al. 2023). Our results corroborate that the species distribution is clearly limited by summer and winter temperature and calcium content, *i.e.*, it prefers base-rich sites in cold climates. Nevertheless, Schenková and Horsák (2013a) reported that *V. genesii* can occur in fens with calcitolerant peat mosses of *Sphagno warnstorfii-Tomenthypnion alliance*, *i.e.*, the habitat most frequently inhabited by the acidophilous *V. lilljeborgi* (see Horsák et al. 2017). Likewise, our dataset includes 32 sites where *V. genesii* and *V. lilljeborgi* occurred sympatrically. However, it is likely that these species occupied different micropatches of the sampled plot. All these sympatrical occurrences come from Fennoscandia where it is more common for types of mires with varying mineral richness to co-occurr and intermingle at small spatial scales (Rydin et al. 1999). Colder climate in Fennoscandia counteracts the competitive ability of *Sphagnum* species in rich fens (Hájek et al. 2022) and hence supports the co-existence of non-sphagnaceous fen mosses (so called "brown-mosses") and *Sphagnum* spp. Therefore, *V. genesii* most likely dwelled in more alkaline patches (dominated by "brown-mosses") while *V. lilljeborgi* occupied more acidic patches (dominated by *Sphagnum* spp.) as the sampling was done on 16 m^2, *i.e.*, area that can be in some cases very heterogeneous in physiochemical conditions (*e.g.*, Joosten et al. 2017). Our results confirm that it prefers calcium-rich sites, however, it spans a relatively wide range along the mineral richness gradient and appears to be less calciphilous than its congener *V. geyeri*. The need for highly alkaline sites reported by Killeen (2003) is therefore probably true in England and Scotland where this publication originated. Out of the three analysed species, it prefers the least waterlogged and vegetation-productive sites. The need for lower summer temperatures is likely one of the reasons for its very rare and scattered distribution in temperate Europe. This is also consistent with earlier literature describing the species as boreo-alpine (Kerney et al. 1983) or arctic-alpine (Cameron et al. 2003), as low temperatures are typical for high altitudes. Even in northern Europe, the species' optimum is at higher altitudes, although, it also occurrs in subalpine region (von Proschwitz 2003; von Proschwitz et al. 2023). An exception, however, is the occurrence of *V. genesii* at considerably lower altitudes between 75 and 525 m a.s.l. in the United Kingdom (Killeen 2003; Killeen et al. 2019). Therefore, global warming associated with ongoing climatic change (Essl et al. 2012) poses a serious threat for this species, together with human-induced eutrophication as the species prefers nutrient-poor sites.

Vertigo geyeri

Distribution

Historical records of *V. geyeri* are summarized in Kerney et al. (1983), showing that it is widespread especially in Sweden, with relatively frequent but regionally restricted occurrence in Norway, Finland (see also von Proschwitz 2003; von Proschwitz et al. 2023 for distribution in Scandinavia), Denmark, Slovakia, United Kingdom, and in the Alps in Germany, Austria, and Switzerland. During the 1990s and after the 2000s after the species was listed in Annex II of the EU Habitats Directive (92/43/EEC), the interest in the distribution of *V. geyeri* started to grow and many new sites were discovered. The species is considerably more common in the Baltic States (data presented here; GBIF.org; Skujiene et al. 2019 2020 2021) than previously reported, similarly as in the United Kingdom and Denmark (Killeen et al. 2019; Conchological Society of Great Britain & Ireland 2020). Most of the findings from Poland come from the northeastern part (data presented here; Książkiewicz et al. 2015; Pokryszko et al. 2016), an area where the Scandinavian ice sheet advanced during the LGM (Hughes et al. 2013). Outside of its main area of distribution in the arctic and boreal zones, many new sites were discovered. Since the first record in 2011, *V. geyeri* was discovered at several sites in Czechia (data presented here; Myšák et al. 2012; Schenková and Horsák 2013b; Horsáková and Horsák 2018; Coufal 2019; Čejka et al. 2020) and the originally known range in the Western Carpathians (mainly Slovakia) was repeatedly revisited and extended

(Schenková et al. 2012). Several isolated sites were discovered in the Romanian Carpathians (data presented here), probably marking the southeasternmost edge of the distribution. Several sites further south on the Balkan peninsula were explored, *e.g.*, in Serbia, Montenegro, and Bosnia and Herzegovina, however, these yielded very poor mollusc communities without any demanding wetland species (unpubl. data). This is likely due to the young age of local groundwater-fed mires which originated later during the Holocene because the glacial period and the beginning of the Holocene were very dry (Wright et al. 2003). However, it is possible that *V. geyeri* is more common in the Romanian Carpathians as there are more suitable unexplored sites (*e.g.*, Hájek et al. 2021). The two records from Ukraine were published before 1950, as mentioned in Gural-Sverlova and Gural (2012). However, Balashov (2016) reported that these populations went extinct due to the destruction of the sites by illegal amber mining. Nevertheless, it is possible that the species still occurs in Ukraine elsewhere, for example in the Carpathian Mountains as ecologically suitable sites are present there (*e.g.*, Hájek et al. 2021). This is also suported by a record of subfossil shells from the sediments dated back to 621–256 cal. yrs BP near Yunashkiv, Western Podillia (Hájková et al. 2022). In the calcareous areas of the Alps, mainly in Switzerland and France, but also in Austria (data presented here; Lecaplain 2013; Roy and Vanderpert 2016; Claude and Gonseth 2021; Lasne et al. 2021), the previously known range was extended. Nevertheless, the species is likely to be even more frequent there. The southernmost known records come from the Apennine Mountains in Italy (data presented here). However, ecologically suitable habitats occurr also in the Pyrenees and in Cantabria (Jiménez-Alfaro et al. 2014; Chytrý et al. 2020). Nevertheless, no records of the species are known from this area, possibly due to the lack of malacological surveys focusing on spring fens.

Ecology

According to older literature, *Vertigo geyeri* inhabits neutral to base-rich, calcareous groundwater-fed wetlands, while in Karelia it has also been found in wet, open deciduous forests (Kerney et al. 1983; Cameron et al. 2003; Valovirta 2003; von Proschwitz 2003; von Proschwitz et al. 2023). Microhabitat preferences were studied by Kuczyńska and Moorkens (2010), while Horsák and Hájek (2005) and Schenková et al. (2012) studied its habitat preferences on the regional scale in the Western Carpathians. The latter two studies used data (n = 20; n = 57; respectively) that are a subset of this study (n = 222). Schenková et al. (2012) showed that climatic predictors have a significant contribution to the ecological gradient along a PCA axis. Although *V. geyeri* is often described as a boreo-montane species (Kerney et al. 1983; Cameron et al. 2003; von Proschwitz 2003), *i.e.*, occurring in areas with lower temperatures, it also frequently inhabits regions with low to intermediate (British Isles; Holyoak 2003; Killeen 2003; Killeen et al. 2019) and intermediate altitude (*e.g.*, Western Carpathians and Czechia; Schenková et al. 2012; Coufal 2019). Accordingly, our data show that *V. geyeri* prefers sites with higher summer and winter temperature (in comparison with *V. lilljeborgi* and *V. genesii*) while the abundances are highest at sites with summer temperature around 21°C. This is most likely one of the primary reasons why this species is substantially more common in temperate Europe than the other two relict species. Schenková et al. (2012) showed a decreasing abundance in response to increasing nutrient availability. The reason behind this is that the temperate sites used in the study are more productive (*e.g.*, Horsák et al. 2017) compared to our dataset that includes sites from northern Europe, making this trend only weak in our data. This might also be due to the wider ecological niche of northern populations as the species was reported to occurr there in wet open deciduous woodlands (Pokryszko 2003; Valovirta 2003; von Proschwitz 2003) whereas it has never been observed in such a habitat in temperate Europe. The decrease in opennes in spring fens means encroachment by shrubs and trees which is often caused by habitat succession towards more productive ecosystems (*e.g.*, Jensen and Schrautzer 1999; Jamrichová et al. 2014). Our results show that the species has a broad tolerance along the mineral richness gradient, as shown in previous studies (Horsák and Hájek 2005; Vavrová et al. 2009; Schenková et al. 2012). Horsák and Hájek (2005) show a unimodal response of the species abundance peaking around 360 μS/cm while our data show a peak at 500 μS/cm, which is consistent with Schenková et al. (2012). The discrepancy is likely due to a smaller dataset used in Horsák and Hájek (2005). The results of our analyses do not show a significant relationship between the species occurrence/densities and moisture as shown in Kuczyńska and Moorkens (2010) and Schenková et al. (2012), however, this is likely due to the size of our dataset and the selection of sites that are well within the species ecological range.

CONCLUSIONS

Our results show that these endangered species have more frequent distribution in temperate Europe than expected and previously known. This is especially true for *V. geyeri* that is regionally frequent in many areas of central and western Europe. However, there are still areas that are poorly explored and can potentially harbor undiscovered populations of these threatened species, such as the Pyrenees and the Cantabrian Mountains.

Vertigo lilljeborgi and especially *V. genesii* seem to be restricted to areas with lower temperatures, therefore, the rising temperature associated with climate change likely poses a serious threat to these species. It was shown that groundwater-fed fens represent a microclimatic refuge as the upwelling water is able to alleviate the effects of macroclimate and provide microclimatically stable conditions (Horsák et al. 2021; Coufal et al. 2023). Nevertheless, some studies suggest that even the shallow groundwater temperature is going to increase (Kurylyk et al. 2013; Mengberg et al. 2014), potentially challenging this temperature-buffering effect. *Vertigo geyeri*, on the other hand, prefers higher temperatures and it is therefore expected to be more resilient to the temperature increase. Nevertheless, as a species sensitive to water level drop and fluctuation (Kuczyńska and Moorkens 2010; Schenková et al. 2012), it is likely to be threatened indirectly via the expected decrease in groundwater (Essl et al. 2012). Similarly to *V. genesii*, it inhabits calcium-rich sites, although the former tolerates a wider alkalinity range with an optimum at higher values than the latter. *Vertigo lilljeborgi*, on the other hand, is restricted to calcium-poor, neutral- to slightly low pH sites.

Despite the increase in known sites, the distribution of these three species in temperate Europe is bound to relict sites with long historical continuity. These habitats are scattered over areas with suitable climate, and most of them are small patches that are sensitive to human-made changes, such as eutrophication and drainage. Thus, the sites in temperate Europe should be strictly protected to prevent any changes that would compromise the water regime stability and the low-productive, nutrient-limited state of vegetation that is crucial for the habitat preservation. For sites with the presence of *V. geyeri* and *V. genesii* that are included in Annex II of the EU Habitats Directive (92/43/EEC) and are regarded species of community interest, special areas of conservation should be designed. Sites with *V. lilljeborgi* should be strictly protected in a similar manner as it has an equal conservation value and similarly acts as an umbrella species.

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Supplementary materials

Fig. S1. Generalized Linear Models (GLMs) performed on binary data (presence/absence) of all species and analysed environmental predictors. Shaded stripes indicate 95% confidence interval. Non-significant relationships and relationships explaining < 10% variation (Adj. R^2) are faded. (download)

Table S1. List of personal unpublished records. The list includes geographical coordinates, country, nearest settlement, description of locality, classification to fen category according to Hájek et al. (2006), date and name of the collector(s). (download)