Refugial occurrence and ecology of the land-snail *Vertigo lilljeborgi* in fen habitats in temperate mainland Europe

Michal Horsák[1*], Michal Hájek[1], Veronika Horsáková[1], Jaroslav Hlaváč[2], Petra Hájková[1], Daniel Dítě[3], Tomáš Peterka[1], Jan Divíšek[1], Anna Potůčková[4] and Richard C. Preece[5]

[1] *Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czech Republic*

[2] *National Museum in Prague, Zoological Department, Václavské náměstí 68, CZ-11579, Prague 1, Czech Republic*

[3] *Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Dúbravská cesta 9, SK-845 23 Bratislava*

[4] *Department of Botany, Charles University in Prague, Benátská 2, CZ-12801 Prague, Czech Republic*

[5] *Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*

*Correspondence: M. Horsák; e-mail: horsak@sci.muni.cz

Short running head: *VERTIGO LILLJEBORGI* IN MAINLAND EUROPE

ABSTRACT

Vertigo lilljeborgi (Westerlund, 1871) is one of the rarest terrestrial snail species in temperate mainland Europe, traditionally considered a glacial relict there. This contrasts with its occurrence in northern Europe where it is a widespread species. This species prefers constantly wet habitats that are neutral to slightly acidic, and avoids highly alkaline conditions, which is an extremely rare ecology for a Eurasian mollusc. Until 2012, only five historical records of this species were known in mainland Europe to the south of its main distribution in northern Europe. Since then, 20 new sites have been discovered, mostly located in the Hercynian Mountains (Bohemian Massif in the Czech Republic and Massif Central in France). In comparison with the boreal European and Alpine populations, those from the Hercynian Mountains inhabit acidic, rather soligenous and productive fens, strongly dominated by *Sphagnum*. *Vertigo lilljeborgi* does not occur in some sites with apparently suitable habitats as indicated by species composition of the vegetation. We observed a surprising correspondence between the occurrence of *V. lilljeborgi* and mean July air temperature and we report its first fossil record from the last glacial period from Central Europe. Although the number of its sites has increased recently, these sites represent unusual and highly unique habitats, vulnerable to drainage and destruction from human activities. This calls for a need of conservation efforts in most of the newly discovered isolated sites.

INTRODUCTION

Several land snail species can be considered characteristic of temperate Europe during full-glacial periods based on their frequency in Pleistocene loess deposits and their extreme rarity in modern communities (Ložek, 2001; Horsák, Juřičková & Picka, 2013). Today, most of these species have typical arctic-alpine distributions, being widely dispersed across Fennoscandia with a few relict populations surviving at high elevations in Central Europe (e.g. Horsák *et al.*, 2015). Some isolated populations also persist in environmentally stable habitats, such as mires, in lowland regions (Schenková & Horsák, 2013).

Vertigo lilljeborgi (Westerlund, 1871) is one of these species, which in temperate mainland Europe is restricted to open peat-forming wetlands with slightly acidic or near neutral pH values (e.g. Horsák *et al.*, 2013). This snail has an almost continuous distribution in Northern Europe, north of about 55° (Kerney, Cameron & Jungbluth, 1983; Welter-Schultes, 2012). There, and also in the British Isles, it commonly occurs in other habitats such as marshes and alder carrs at the margins of lakes and rivers (Kevan & Waterston, 1933; Kerney *et al.*, 1983). Only a few isolated populations have been reported from mainland Europe south of 55° N down to the Pyrenees (see Schenková & Horsák, 2013 for the review of records). Its distribution also stretches across the entire Eurasian taiga and tundra zones (Sysoev & Schileyko, 2009; Horsák & Chytrý, 2014) with isolated records from the Altai Mountains (Meng, 2008) and the Hokkaidō (Nekola *et al.*, in press). It also occurs in NE North America from northern Maine to the central Québec - Labrador border, where based on phylogenetic data these populations were described as a distinct subspecies (Nekola *et al.*, in press).

This study summarizes and assesses all the modern and fossil records of this species across temperate mainland Europe, including several new records with a high conservation value. We also characterise its ecological requirements based on all currently known populations in temperate mainland Europe, and compare them with data from Scandinavia and the Baltic countries collected across the same spectrum of habitats and with the same sampling protocol. Using vegetation samples recorded from the same sample plots, we attempt to characterise the vegetation and habitat conditions preferred by this species within mire habitats.

MATERIAL AND METHODS

Study sites and field sampling

We investigated 583 pristine fen sites (treeless wetlands, mostly situated on groundwater seepages) covering the whole ecological range of these habitats (e.g. Hájek *et al.*, 2006). The study sites are distributed across mainland Europe and clustered in the regions where fen habitats are frequent. The sampling was undertaken in 2001–2016, but all data on *V. lilljeborgi* were collected between 2012 and 2016. In the central part of each site a sampling plot of 4 × 4 m of homogeneous vegetation was delineated from which data on the molluscs, vascular plants and bryophyte species were collected. From each plot, one 12-L sample of the uppermost fen layer was collected for molluscs. Shells were extracted from samples using a wet sieving technique performed in the field (Horsák, 2003). Samples were dried in the laboratory, and shells were hand-sorted and identified under a dissecting stereomicroscope. The species composition of vascular plants and bryophytes from each plot was recorded on the nine-point Braun-Blanquet scale (Van der Maarel, 1979). Vascular plant species-level identifications were mostly conducted in the field, whereas bryophyte identifications were mostly verified in the laboratory.

Environmental predictors

Geographical coordinates of each plot were recorded using the Garmin 60CSx GPS device. Water conductivity and water pH were measured directly in the field at each sampling plot using portable instruments. Conductivity caused by H^+ ions in acidic waters (pH < 5.5) was subtracted (Sjörs, 1950). Water pH and calcium concentration, as reflected by water electric conductivity (see Horsák, 2006), were found to have a synergistic control on vegetation structure (brown mosses vs. *Sphagnum* mosses; Vicherová, Hájek & Hájek, 2015) to which mollusc species respond. Therefore, we combined water pH and water conductivity (a proxy for calcium richness) into a single variable, hereafter called adjusted pH, using the formula presented in Plesková *et al.* (2016). For each site, a set of climatic variables (i.e. mean annual air temperature, annual precipitation amount, mean January air temperature, and mean July air temperature) was obtained from the WorldClim database v. 1.4 (Hijmans *et al.*, 2005) using the ArcGIS 8.3 program (ESRI, 2013).

For each plot we also summed the percentage cover of species that indicate semi-aquatic conditions of waterlogged topogenous (quaking) fens as our previous study (Schenková *et al.*, 2014) found that severe waterlogging can have a strong effect on fen molluscs. Here we used indicator species groups based on a pan-European phytosociological synthesis of fen vegetation (Peterka *et al.*, 2017; Appendix S4 in Supporting Information). We united species' groups named *Carex elata*, *Carex limosa*, *Scorpidium scorpioides*, *Menyanthes trifoliata*, and *Sphagnum cuspidatum* (see Appendix S4 in Peterka *et al.*, 2017 for individual plant species) and added purely aquatic plants (*Potamogeton*, *Utricularia*, and *Lemna*). The value of summed percentage cover of these plant species was used in a multidimensional analysis as the measure of fen types on a scale from soligenous to topogenous conditions.

Selection of suitable sites using vegetation data

We assembled all current data on *V. lilljeborgi* occurrence from temperate mainland Europe consisting of 19 sites in the Czech Republic, Switzerland and France (hereafter referred to as Temperate Europe). These data were collected using the same sampling protocol and accompanied by the same set of environmental and climatic predictors. To explore whether any ecological differences exist between highly isolated and scattered populations in Temperate Europe and north European regions of the species' continuous distribution (Kerney *et al.*, 2013; Waldén, 2007), we used 24 samples from Norway, Sweden and Baltic countries (referred to as Boreal Europe) collected under the same protocol as for Temperate Europe. Although the species has been found in Boreal Europe in a variety of habitats, we limited our samples to open mire habitats to make these two datasets comparable. We determined the plant species that differentiate vegetation supporting *V. lilljeborgi* as opposed to the mires sampled for molluscs where *V. lilljeborgi* was absent. The six most important species (according to phi-coefficient calculation) were selected for both the Boreal European and Temperate European subset, with the species significant at $P<0.001$ in Fisher's exact test having a priority in the selection (Table 1).

In addition, we calculated the Frequency-Positive Fidelity Index (FPFI; Tichý, 2005) to the group of samples with *V. lilljeborgi*, again separately for the Boreal European and Temperate European subsets, for each of the 583 samples where both vegetation and molluscs were recorded. We repeated this approach also for the large pan-European dataset of fen vegetation samples collected for the study of Peterka *et al.* (2017) and consisting of 24,091 vegetation-plot records. The vegetation plots from this dataset were considered similar at the threshold of FPFI of 40 (for Temperate European subset) or 32 (Boreal European subset). These thresholds correspond to the inflexion point of the power law curve of FPFI values calculated for both regions. Similar samples were mapped as potentially suitable sites for *V. lilljeborgi*.

Statistical analyses and mapping techniques

To investigate the affinity of *V. lilljeborgi* to any fen vegetation type, we subjected the vegetation samples to Multidimensional Scaling (MDS; = Principal Coordinates Analysis) based on Bray-Curtis dissimilarity to explore the main gradients of compositional variance. To associate this composition variance with the adjusted pH and water regime we fitted these values into the two dimensional ordination space using the "ordisurf" function from the "vegan" package (Oksanen *et al.*, 2013).

The distribution of *V. lilljeborgi* was assembled from published literature (Kerney *et al.*, 1983; Schenková & Horsák, 2013) and augmented with our new records from the Baltic countries (2014 data) and from Central Europe (Fig. 1, Appendix S1). We also assembled all fossil records post-dating the Last Glacial Maximum in order to evaluate its presumed relict status in Central Europe.

RESULTS AND DISCUSSION

Modern distribution in temperate mainland Europe

The species has been documented from 25 isolated sites in temperate mainland Europe (Fig. 1; Table S1 in Appendix 1), including several new records from the southwestern part of the Czech Republic (Schenková & Horsák, 2013) and the Massif Central in France (Vrignaud, 2012; Lecaplain, 2013). Four very isolated sites were recently also found in the Swiss and French Alps (Schenková & Horsák, 2013, Combrisson & Vuinée, 2017). All these 20 recently discovered populations have been found since 2011. The remaining five sites are based on older records (1921-1979) from southern French Pyrenees (van Regteren Altena, 1934), southeastern Spanish Pyrenees (von Proschwitz, 2004), and northeastern, southwestern, and southeastern Germany (Schmierer, 1921; Hässlein, 1964; Gerber, 1987). Another recent record from the margin of the French Alps (Thomas, 2015) is most likely based on a misidentification of *Vertigo pygmaea* since the image of the specimen and the habitat match that species far better. Apart from these records, there are also isolated sites for this snail in western coastal Denmark (von Proschwitz, 2003), which are located close to its continuous distribution in Fennoscandia (Fig. 1).

Ecological requirements: comparison of Temperate and Boreal European populations at fen habitats

As reported in the literature (Kerney *et al.*, 1983; Horsák *et al.*, 2013; Schenková & Horsák, 2013, Nekola *et al.*, in press), this species inhabits wetlands with a high water-table and neutral to slightly acidic water chemistry (Table 1 and 2; Fig. 2a, b). It occurs in a variety of habitats from treeless peat-accumulating sites to tall sedge communities at the margins of lakes and rivers and it even inhabits open riparian woodlands (e.g. Kerney *et al.*, 1983). It this study we focus solely on its ecology within fen habitats as all currently known populations in mainland temperate Europe are limited to these. We found that the land-snail assemblages of treeless fen sites containing it were mostly species-poor (on average 5 spp., varying between 1 and 14 spp.). In total 33 land-snail species were recorded in 43 plots with *V. lilljeborgi* distributed across mainland Europe, although only five species were common (Table S2 in Appendix). Interestingly, in some plots with *V. lilljeborgi* some calcium-demanding species (e.g. *Vertigo genesii*) were also recorded. These were either transitional sites with water chemistry within the tolerance range of both species, or heterogeneous sites with patchy chemistry determined by the distribution of *Sphagnum* mosses that acidify the environment and accumulate rainwater. We found no statistical differences between the sites with and without the species based on annual precipitation and mean January air temperature (Fig. 2c, d). By contrast, we found a strong difference based on mean July air temperature, with occupied sites being significantly colder (Fig. 3). There was also a clear pattern in species abundance variation, showing a bell-shaped response to July air temperature (Fig. 3). Increasing summer temperatures generally increase plant productivity and hence may support an abundance of secondary producers, but very high summer temperatures decrease depth to water-table because of increasing evapotranspiration (e.g. Gorham, 1974; Moradi *et al.*, 2012; Navrátilová *et al.*, 2017). These facts fit our observations in the field and may explain the pattern for July temperature and *V. liljeborgii* abundance.

We found that differences exist between Temperate and Boreal European populations in habitat conditions and vegetation composition (Table 1, 2; Fig. 4). The vegetation at three sites in the Alps was more similar to that in Boreal Europe, especially in the Mauntschas Mire near St. Moritz, which plotted in the middle of the Boreal European cluster in the MDS analysis (Fig. 4). The populations of *V. lilljeborgi* from Boreal Europe and the Alps frequently inhabit: (i) brown-moss quaking (topogenous) fens dominated by *Scorpidium scorpioides* and other non-sphagnaceous mosses with boreal ranges (the *Stygio-Caricion limosae* alliance); and (ii) rich fens with brown-mosses (*Tomentypnum nitens*, *Paludella squarrosa* and *Campylium stellatum*) and calcium-tolerant *Sphagnum warnstorfii* (the *Sphagno-Tomentypnion* alliance, for further details see Peterka *et al.*, 2017). In a few cases *V. lilljeborgi* even occurred in calcareous brown-moss fens of the *Caricion davallianae* alliance (Table 2). The Boreal European fens were generally more waterlogged (Fig. 4) and characterised by a group of boreal species of low-productive habitats, including dwarf shrubs

Andromeda polifolia and *Betula nana*, the circumpolar sedge *Carex livida*, and the bryophytes *Lophozia borealis* and *Cinclidium stygium* (Table 1). In contrast, Hercynian populations (Bohemian Massif and Massif Central) preferred more acidic, usually soligenous fens that were strongly dominated by *Sphagnum* (the *Caricion fuscae* and *Sphagno-Caricion canescentis* alliances, Table 2). Generally they were also characterised by the occurrence of productive sedges and herbs of strongly waterlogged or littoral conditions (*Potentilla palustris* and *Carex rostrata*), as well as calcifuge wetland generalists (*Carex canescens* and *Juncus filiformis*). Some of these species are quite nutrient-demanding (*Carum verticillatum*, *Calliergon cordifolium* and *Epilobium palustre*) and floristically similar to flooded fens (Navrátilová *et al.*, 2017). Such littoral sites are similar to many sites where it occurs in the British Isles and northern Europe (Kerney *et al.*, 1983; B. Coles, pers. comm.).

Late-glacial-early Holocene records and relict status

Vertigo lilljeborgi has often been considered a glacial relict (e.g. Jaeckel, 1962), but the fossil evidence is too sparse to provide any support for this. This is not really surprising since any snail species that specifically avoids calcium-rich environments is very unlikely to be preserved in calcareous deposits such as loess (Ložek, 2001). Its presumed relict status is based largely on its rare and scattered modern distribution in temperate mainland Europe, in contrast to its continuous distribution in northern Europe, where it occurs together with other glacial species characteristic of loess communities (Horsák *et al.*, 2015). The only fossil records from mainland Europe come from Germany and Poland (Jaeckel, 1962) but these records are old, unverified and poorly dated. Because some of these specimens were recovered from loess it is likely that they have been misidentified since this species has not been subsequently found in loess deposits in Germany (S. Meng, pers. comm.) or in the former Czechoslovakia, where several hundred sequences have been studied (Ložek, 1964, 2001). There are a few fossil records of *V. lilljeborgi* from the British Isles, all of which were recovered from calcareous silts or tufas, which afford the best preservation potential. Three of these sites are of late-glacial age (Mitchell, 1951; Thew, Gilbertson & Woodall, 1984; Garnett *et al.*, 2006) and three are early Holocene tufas (Preece & Robinson, 1982, 1984; Preece, Coxon & Robinson, 1986). These records are often only based on single shells, suggesting that this species did not inhabit the calcium-rich areas where the deposits formed but were transported there from nearby acidic habitats. It is interesting to note that another calcifuge snail, *Zonitoides excavatus*, regularly occurs in Holocene (and interglacial) tufas in the British Isles, suggesting that acidic habitats and tufa-forming environments could occur in close proximity. The first reliable late-glacial record of *V. lilljeborgi* from Central Europe has recently been discovered from a tufa in southern Slovakia (48°10'12.2"N, 18°45'23.5"E, Santovka-BP, M. Horsák det.). This shell has been dated to 14 197 cal. yrs BP (UGAMS-18226; 12280±30 ^{14}C years BP) based on AMS dating of associated seeds of *Schoenoplectus tabernaemontani*. This suggests that *V. lilljeborgi* only occurs at sites with specific environment parameters and/or history.

Potential distribution and conservation remarks

We observed that the variation of potentially favourable mire vegetation for *V. lilljeborgi* seems to be more heterogeneous in Temperate Europe than in Boreal Europe (Fig. 5). This pattern is partly caused by greater sampling effort in Temperate Europe, inevitably making individual samples dissimilar. We also did not cover the full range of occupied vegetation types in Boreal Europe as we limited our sampling to mire habitats, thus the samples from Boreal Europe may only serve for a comparison with those from Temperate Europe. Thus, the most important result of this analysis is that despite greater heterogeneity of Temperate European samples, those with *V. lilleborgi* from the Hercynian Mountains (right part of the envelope in Fig. 5) formed a distinct, compositionally uniform group. This suggests that *V. lilljeborgi* only occurs at sites with specific environment parameters and/or history.

Suitable habitats with appropriate vegetation occur not only in the regions where *V. lilljeborgi* occurs (Bohemian Massif, Massif Central, Western Alps, Northern Europe), but also in regions where it has never been found (Northern European Plain, Carpathians and neighbouring Eastern Sudetes, eastern Alps; Fig. 6). Some of these regions (e.g. Western Carpathians; Fig. 6) have been subjected to extensive sampling. Even within the Temperate European regions where it occurs, it does not occupy all suitable sites. This suggests dispersal limitation and its pattern of occurrence seems to be affected more by extinction than by migration events, which may further support its relict status. The reasons for its absence in some areas may be linked with the Holocene history of these regions (e.g. a young history of *Sphagnum*-rich fens, the existence of forested phases in the mid Holocene, Hájková *et al.*, 2012) or with environmental deterioration that occurred during the Industrial Age (e.g. Navrátilová *et al.*, 2017).

For some fens where both historical and recent vegetation data were available, such as the Suchdol fen in the Bohemian Massif (Rybníček, 1974), we found that historical plot(s) display greater similarity to the Boreal European than to the Temperate-European cluster with *V. lilljeborgi* (data not shown). This result suggests that the Temperate European cluster of samples with *V. lilljeborgi* represents successionally shifted vegetation that developed from boreal-like fens, which still occur in Northern Europe. The change from rich fens with brown mosses and *Sphagnum warnstorfii* to fens encroached by late-successional, competitive *Sphagnum* species (i.e. *S. teres, S. flexuosum, S, fallax* and *S. palustre*) have recently been described from the Bohemian Massif (Hájek *et al.*, 2015; Navrátilová *et al.*, 2017). *Vertigo lilljeborgi* is still relatively frequent in the Bohemian Massif and Massif Central, but this distribution may represent an extinction debt because of ongoing successional changes. Based on field observations and historical data on vegetation it is probable that *V. lilljeborgi* was more common in these two regions until about the 1960s and 1970s, where it inhabited all suitable habitats. In both regions most of these mire habitats have been severely damaged or destroyed by human impacts, such as drainage, agriculture, eutrophication, human-induced succession. In the Massif Central, we found populations surviving in small remnants of originally much larger fens, now being destroyed by cow pasture. Remnant healthy populations are also linked with mires at lake shores. In the Czech Republic, all known populations except two were found in state-protected areas, representing the last remnants of a habitat type that was frequent in the landscape until only a few decades ago. The marked increase of records for *V. lilljeborgi* in temperate mainland Europe over the last five years is associated purely with the increased research effort and interest in these habitat types, which had been overlooked by malacologists. The same is true for other fen snail species, such as *Vertigo geyeri* and *V. genesii* (e.g. Schenková *et al.*, 2012; Schenková & Horsák, 2013). In the case of these two species, the increasing interest and number of new findings are directly linked with their protection under Annex II of the European Union's Habitat Directive (92/43/EEC), which has resulted in monitoring programmes across the EU. Although the number of known sites is increasing, the total number of both actual and potential habitats of these species has decreased dramatically in most regions as documented by floristic surveys (Navrátilová *et al.*, 2017) and old malacological records (e.g. Schmierer, 1921).

To summarise, *Vertigo lilljeborgi* appears to be a species of narrow and clearly defined ecological preferences in temperate mainland Europe. Isolated, and often declining, populations in this part of Europe are likely to be relictual and thus worthy of strict conservation effort. In northern Europe and in the British Isles it occupies a wider range of habitats (e.g. Kerney *et al.*, 1983), and is regarded as Not Threatened (Cuttelod, Seddon & Neubert, 2011).

ACKNOWLEDGEMENTS

We are very grateful to Eva Boyer, Xavier Cucherat, Jan Myšák and Luboš Beran for sharing their original records of *V. lilljeborgi*. Ondřej Hájek helped with climatic data. Brian Coles and an anonymous reviewer made many valuable comments to the first draft of the paper. The paper was supported by the Charles University Grant Agency (GAUK/204215), the Research Plan of the National Museum in Prague (DKRVO2017/15), and mainly the Czech Science Foundation (GACR/17-05696S).

REFERENCES

COMBRISSON, D. & VUINÉE L. 2017. Note sur la présence du vertigo des aulnes *Vertigo lilljeborgi* (Westerlund, 1871) sur le massif du Taillefer en Isère (France). *MalaCo*, **13**: 5-7.

CUTTELOD, A., SEDDON, M. & NEUBERT, E. 2011. *European Red List of Non-marine. Molluscs*. Publications Office of the European Union, Luxembourg.

ESRI. 2013. *ArcGIS 8.3*, Environmental Systems Research Institute, Redlands, CA, USA. Available at: http://www.esri.com.

GARNETT, E.R., ANDREWS, J.E., PREECE, R.C. & DENNIS, P.F. 2006. Late-glacial and early Holocene climate and environment from stable isotopes in Welsh tufa. *Quaternaire*, **17**: 31-42.

GERBER, J. 1987. Ein Glazialrelikt im Schwarzwald: *Vertigo lilljeborgi* (Westerlund, 1871)(Gastropoda, Vertiginidae). *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz*, **14**: 321-324.

GORHAM, E. 1974. The relationship between standing crop in sedge meadows and summer temperature. *Journal of Ecology*, **62**: 487-491.

HÁJEK, M., HORSÁK, M., HÁJKOVÁ, P. & DÍTĚ, D. 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspectives in Plant Ecology, Evolution and Systematics*, **8:** 97-114.

HÁJEK, M., JIROUŠEK, M., NAVRÁTILOVÁ, J., HORODYSKÁ, E., PETERKA, T., PLESKOVÁ, Z., NAVRÁTIL, J., HÁJKOVÁ, P. & HÁJEK, T. 2015. Changes in the moss layer in Czech fens indicate early succession triggered by nutrient enrichment. *Preslia*, 87: 279-301.

HÁJKOVÁ, P., HORSÁK, M., HÁJEK, M., LACINA, A., BUCHTOVÁ, H. & PELÁNKOVÁ, B. 2012. Origin and contrasting succession pathways of the Western

Carpathian calcareous fens revealed by plant and mollusc macrofossils. *Boreas*, **41**: 690-706.

HÄSSLEIN, L. 1964. Über ein rezentes Vorkommen der nordeuropäisches Schnecke *Vertigo lilljeborgi* Westerlund im Bayrischer Wald. *Bericht der Naturhistorischen Gesellschaft Nürnberg*, **1961/1964:** 66-67.

HIJMANS, R.J., CAMERON, S.E., PARRA, J.L., JONES, P.G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**: 1965-1978.

HORSÁK, M. 2003. How to sample mollusc communities in mires easily. *Malacologica Bohemoslovaca*, **2**: 11-14.

HORSÁK, M. 2006. Mollusc community patterns and species response curves along a mineral richness gradient: a case study in fens. *Journal of Biogeography*, **33**: 98-107.

HORSÁK, M. & CHYTRÝ, M. 2014. Unimodal latitudinal pattern of land-snail species richness across northern Eurasian lowlands. *PLoS ONE*, **9**: e104035.

HORSÁK, M., CHYTRÝ, M., HÁJKOVÁ, P., HÁJEK, M., DANIHELKA, J., HORSÁKOVÁ, V., ERMAKOV, N., GERMAN, D.A., KOČÍ, M., LUSTYK, P., NEKOLA, J.C., PREISLEROVÁ, Z. & VALACHOVIČ, M. 2015. European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas*, **44**: 638-657.

HORSÁK, M., JUŘIČKOVÁ, L. & PICKA, J. 2013. *Měkkýši České a Slovenské republiky. Molluscs of the Czech and Slovak Republics*, Kabourek, Zlín.

JAECKEL, S.G.A. 1962. Ergänzungen und Berichtigungen zum rezenten und quartären Vorkommen der mitteleuropäischen Mollusken. In: *Die Tierwelt Mitteleuropas, Bd. 2* (P. Brohmer, P. Ehrmann & G. Ulmer (Hrsgb.), pp. 25-294. Quelle & Meyer, Leipzig.

KERNEY, M.P., CAMERON, R.A. & JUNGBLUTH, J.H. 1983. *Die Landschnecken Nord- und Mitteleuropas*. Paul Parey, Hamburg and Berlin, Germany.

KEVAN, D.K. & WATERSTON, A.R. 1933. *Vertigo lilljeborgi* (West.) in Great Britain (with additional Irish localities). *Journal of Conchology*, **19**: 296-313.

LECAPLAIN, B. 2013. Découverte du Vertigo des aulnes, *Vertigo lilljeborgi* (Westerlund, 1871) (Gastropoda, Vertiginidae) dans la région Auvergne (France). *MalaCo*, **9**: 451-452.

LOŽEK, V. 1964. *Quartärmollusken der Tschechoslowakei: Mit 32 fotographischen Tafeln*. Nakladatelství Československé akademie věd, Praha.

LOŽEK, V. 2001. Molluscan fauna from the loess series of Bohemia and Moravia. *Quaternary International*, **76**: 141-156.

MENG, S. 2008. Neue Daten zur Verbreitung der Vertiginidae (Gastropoda: Pulmonata) in Zentralasien. *Mollusca*, **26**: 207-219.

MITCHELL, G.F. 1951. Studies in Irish Quaternary deposits: No 7. *Proceedings of the Royal Irish Academy*, **53B**: 111-206.

MORADI, H., FAKHERAN, S., PEINTINGER, M., BERGAMINI, A., SCHMID, B. & JOSHI, J. 2012. Profiteers of environmental change in the Swiss Alps: increase of thermophilous and generalist plants in wetland ecosystems within the last 10 years. *Alpine Botany*, **122**: 45-56.

MUCINA, L., BÜLTMANN, H., DIERßEN, K., THEURILLAT, J.-P., RAUS, T., ČARNI, A., ŠUMBEROVÁ, K., WILLNER, W., DENGLER, J., GARCÍA, R.G. & others. 2016. Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, **19**: 3-264.

NAVRÁTILOVÁ, J., HÁJEK, M., NAVRÁTIL, J., HÁJKOVÁ, P. & FRAZIER, R.J. 2017. Convergence and impoverishment of fen communities in a eutrophicated agricultural landscape of the Czech Republic. *Applied Vegetation Science*, **20**: 225–235.

NEKOLA, J.C., COLES, B.F., CHIBA, S., DROST, T., PROSCHWITZ, T.V. & HORSÁK, M. (in press) A phylogenetic overview of the genus *Vertigo* (Gastropoda: Pulmonata). *Malacologia*.

OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., HENRY, M., STEVENS, H. & WAGNER, H. 2013. *Vegan: Community ecology package. 2013.* R-package version 2.0-10. Available at: http://CRAN.R-project.org/package=vegan.

PETERKA, T., HÁJEK, M., JIROUŠEK, M., JIMÉNEZ-ALFARO, B., AUNINA, L., BERGAMINI, A., DÍTĚ, D., FELBABA-KLUSHYNA, L., GRAF, U., HÁJKOVÁ, P., HETTENBERGEROVÁ, E., IVCHENKO, T.G., JANSEN, F., KOROLEVA, N.E., LAPSHINA, E.D., LAZAREVIĆ, P.M., MOEN, A., NAPREENKO, M.G., PAWLIKOWSKI, P., PLESKOVÁ, Z., SEKULOVÁ, L., SMAGIN, V.A., TAHVANAINEN, T., THIELE, A., BIŢĂ-NICOLAE, C., BIURRUN, I., BRISSE, H., ĆUŠTEREVSKA, R., DE BIE, E., EWALD, J., FITZPATRICK, Ú., FONT, X., JANDT, U., KĄCKI, Z., KUZEMKO, A., LANDUCCI, F., MOESLUND, J.E., PÉREZ-HAASE, A., RAŠOMAVIČIUS, V., RODWELL, J.S., SCHAMINÉE, J.H.J.,

ŠILC, U., STANČIĆ, Z. & CHYTRÝ, M. 2017. Formalized classification of European fen vegetation at the alliance level. *Applied Vegetation Science*, **20**: 124-142.

PLESKOVÁ, Z., JIROUŠEK, M., PETERKA, T., HÁJEK, T., DÍTĚ, D., HÁJKOVÁ, P., NAVRÁTILOVÁ, J., ŠÍMOVÁ, A., SYROVÁTKA, V. & HÁJEK, M. 2016. Testing inter-regional variation in pH niches of fen mosses. *Journal of Vegetation Science*, **27:** 352-364.

PREECE, R.C. & ROBINSON, J.E. 1982. Molluscan and ostracod faunas from Postglacial tufaceous deposits in County Offaly. *Proceedings of the Royal Irish Academy*, **82B**: 115-131.

PREECE, R.C. & ROBINSON, J.E. 1984. Late Devensian and Flandrian environmental history of the Ancholme Valley, Lincolnshire: molluscan and ostracod evidence. *Journal of Biogeography*, **11**: 319-352.

PREECE, R.C., COXON, P. & ROBINSON, J.E. 1986. New biostratigraphic evidence of the Post-glacial colonization of Ireland and for Mesolithic forest disturbance. *Journal of Biogeography*, **13**: 487-509.

VON PROSCHWITZ, T. 2003. A review of the distribution, habitat selection and conservation status of the species of the genus *Vertigo* in Scandinavia (Denmark, Norway and Sweden) (Gastropoda, Pulmonata: Vertiginidae). *Heldia*, **5**: 27-50.

VON PROSCHWITZ, T. 2004. On the distribution and ecology of *Vertigo substriata* (Jeffreys), *Vertigo modesta arctica* (Wallenberg), *Vertigo lilljeborgi* (Westerlund) and *Vertigo alpestris* Alder in France and on the Iberian Peninsula. *Journal of Conchology*, **38**: 411-420.

VAN REGTEREN ALTENA, C.O. 1934. Note sur une récolte de mollusques aux environs de Font-Romeu. *Journal de Conchyologie*, **78**: 262-269.

RYBNÍČEK, K. 1974. *Die Vegetation der Moore im südlichen Teil der Böhmisch-Mährischen Höhe*. Akademie der Wissenschaften, Praha.

SCHENKOVÁ, V. & HORSÁK, M. 2013. Refugial populations of *Vertigo lilljeborgi* and *V. genesii* (Vertiginidae): new isolated occurrences in Central Europe, ecology and distribution. *American Malacological Bulletin*, **31**: 323-329.

SCHENKOVÁ, V., HORSÁK, M., PLESKOVÁ, Z. & PAWLIKOWSKI, P. 2012. Habitat preferences and conservation of *Vertigo geyeri* (Gastropoda: Pulmonata) in Slovakia and Poland. *Journal of Molluscan Studies*, **78**: 105-111.

SCHENKOVÁ, V., HORSÁK, M., HÁJEK, M., PLESKOVÁ, Z., DÍTĚ, D. & PAWLIKOWSKI, P. 2014. Mollusc and plant assemblages controlled by different ecological gradients at Eastern European fens. *Acta Oecologica*, **56**: 66-73.

SCHMIERER, T. 1921. Ein deutscher Fundort für *Vertigo lilljeborgi* West. *Archiv für Molluskenkunde*, **53**: 271-278.

SJÖRS, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. *Oikos*, **2:** 241-258.

SYSOEV, A.V. & SCHILEYKO, A.A. 2009. *Land snails and slugs of Russia and adjacent countries*, Pensoft Publishers.

THEW, N., GILBERTSON, D.D. & WOODALL, D. 1984. Late Devensian molluscan palaeoecology of Holderness. In: *Late Quaternary environments and Man in Holderness* (D.D. Gilbertson, ed.), pp. 109-157. British Archaeological Reports, British Series 134.

THOMAS, A. 2015. Première découverte du *Vertigo lilljeborgi* (Westerlund, 1871) dans la région Rhône-Alpes (Gastropoda, Vertiginidae). *Folia Conchyliologica*, **32**: 19-21.

TICHÝ, L. 2005. New similarity indices for the assignment of relevés to the vegetation units of an existing phytosociological classification. *Plant ecology*, **179**: 67-72.

VAN DER MAAREL, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio*, **39**: 97-114.

VICHEROVÁ, E., HÁJEK, M. & HÁJEK, T. 2015. Calcium intolerance of fen mosses: Physiological evidence, effects of nutrient availability and successional drivers. *Perspectives in Plant Ecology, Evolution and Systematics*, **17**: 347-359.

VRIGNAUD, S. 2012. Inventaire des mollusques de la réserve naturelle nationale de Chastreix-Sancy (Puy-de-Dôme, France). Revue des Sciences Naturelles d'Auvergne, **76**: 39-52.

WALDÉN, H. 2007. *Svensk landmolluskatlas*. Naturcentrum AB, Stenungsund.

WELTER-SCHULTES, F.W. 2012. *European non-marine molluscs: a guide for species identification*. Planet Poster Ed.

Table 1. Vegetation (N=43 plots) most characteristic of sites with *Vertigo lilljeborgi*. The six most important species are listed; those with Fisher's exact test significant at P= 0.001 were given priority.

	Diagnostic species (the best six, if significant at P=0.001)	**The most frequent species (>70%)**
Scandinavian and Baltic fens with *Vertigo lilljeborgi*	*Andromeda polifolia*; *Loeskhypnum badium*; *Lophozia borealis*; *Carex livida*; *Betula nana*; *Cinclidium stygium*	*Campylium stellatum*; *Andromeda polifolia*; *Carex rostrata*; *Eriophorum angustifolium*
Temperate mainland European fens with *Vertigo lilljeborgi*	*Potentilla palustris*; *Carum verticillatum*; *Juncus filiformis; Carex canescens*; *Calliergon cordifolium*; *Epilobium palustre*	*Carex rostrata*; *C. nigra*; *Potentilla palustris*

Table 2. Classification of 43 analysed vegetation plots with *Vertigo lilljeborgi* at the level of vegetation alliances (after Mucina *et al.*, 2016; for details of fen alliances see Peterka *et al.*, 2017). The three best diagnostic species (only if statistically significant based on Fisher's exact test) of each alliance defined in our dataset are shown. Significance of Fisher's exact test: *, 0.05; **, 0.01; ***, 0.001.

Alliance	**The best three diagnostic spp.**	**Regions (number of sites)**
Sphagno warnstorfii-Tomentypnion (rich fens with calcium-tolerant peat mosses)	*Sphagnum warnstorfii**** *Paludella squarrosa**** *Homalothecium nitens***	CZ, Bohemian Massif (1); CH, Alps (1); F, Alps (1); F, Massif Central (1); Baltic countries (6), Scandinavia (11)
Caricion fuscae (moderately rich fens)	*Warnstorfia exannulata**** *Carex canescens**** *Galium palustre****	CZ, Bohemian Massif (3); F, Massif Central (6)
Stygio-Caricion limosae (brown-moss quaking fens)	*Scorpidium scorpioides**** *Carex limosa**** *Euphrasia frigida****	Scandinavia (6)
Sphagno recurvi-Caricion canescentis (poor fens)	*Sphagnum fallax**** *Epilobium palustre**	CZ, Bohemian Massif (3)
Caricion davallianae (calcareous soligenous fens)	*Carex davalliana*** *Salix rosmarinifolia** *Carex hostiana**	F, Alps (1); Baltic countries (1); Scandinavia (1)
Calthion palustris (wet grasslands)	None	CZ, Bohemian Massif (1)

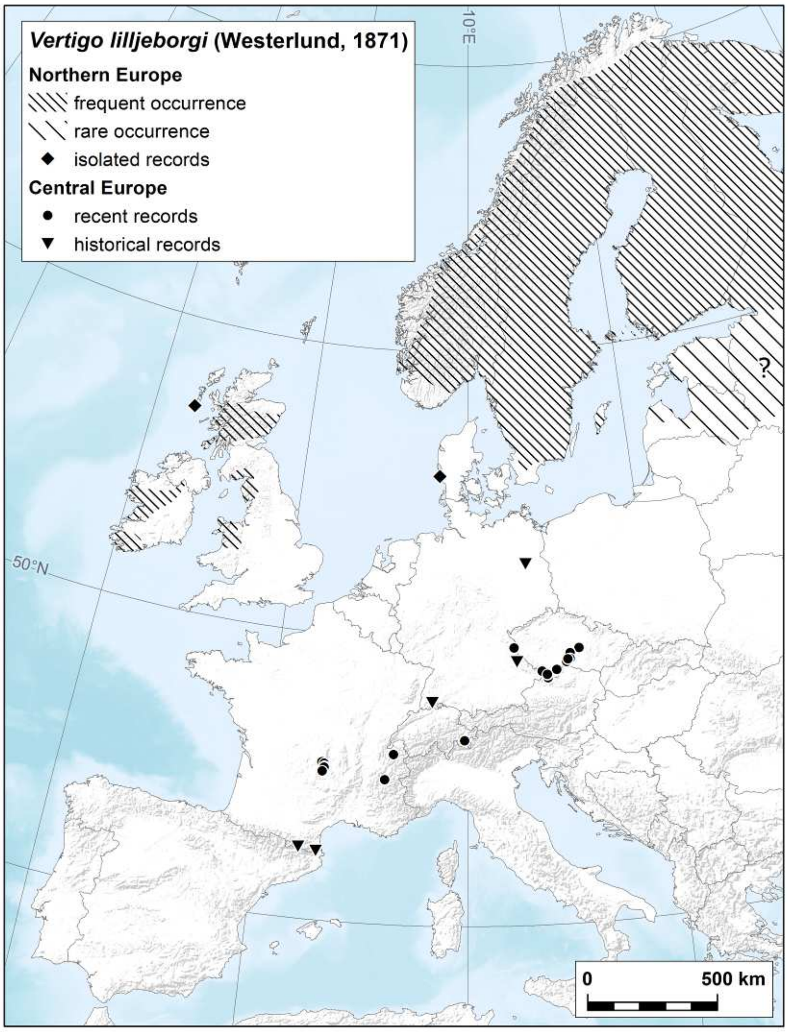

Figure 1. Map of European distribution; adopted from Schenková & Horsák (2013) and updated (see Appendix).

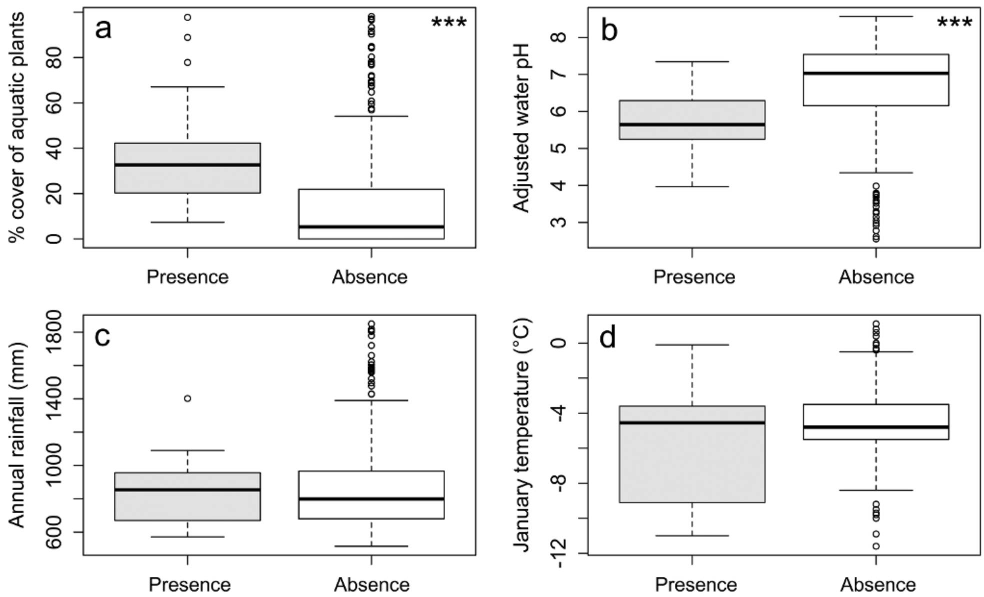

Figure 2. Variation in local (a, b) and climatic (c, d) parameters for the sites with records of *Vertigo lilljeborgi* compared with those measured for the remaining sites out of all 583 fens explored for molluscs. ***, P<0.001 based on Mann-Whitney U tests.

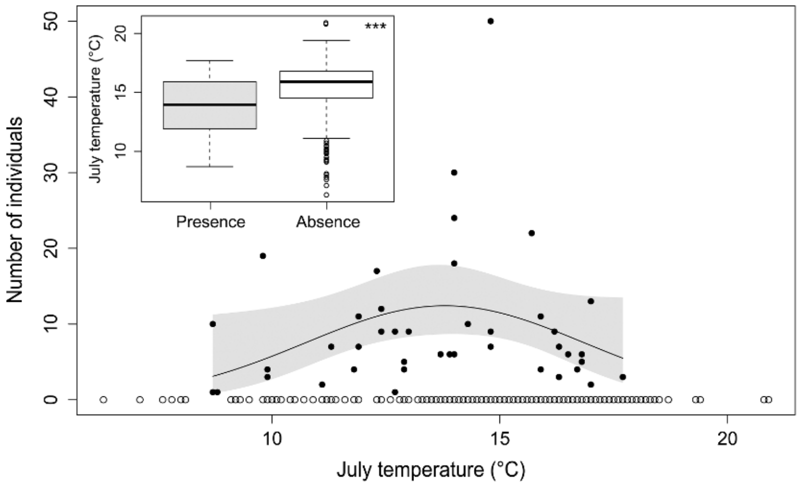

Figure 3. Variation in numbers of *Vertigo lilljeborgi* collected per 12-L sample volume among all 583 study sites in relation to mean July air temperature. Sites with (grey boxplot) and without *V. lilljeborgi* significantly differed in their July temperature (***, Mann-Whitney U tests, P<0.001). Only based on samples with the species (N=43, black circles), the variation of collected individuals was modelled by GLM with quasi-Poisson error structure in relation to July temperature (P=0.038). Grey area shows 95% confidential interval of the model.

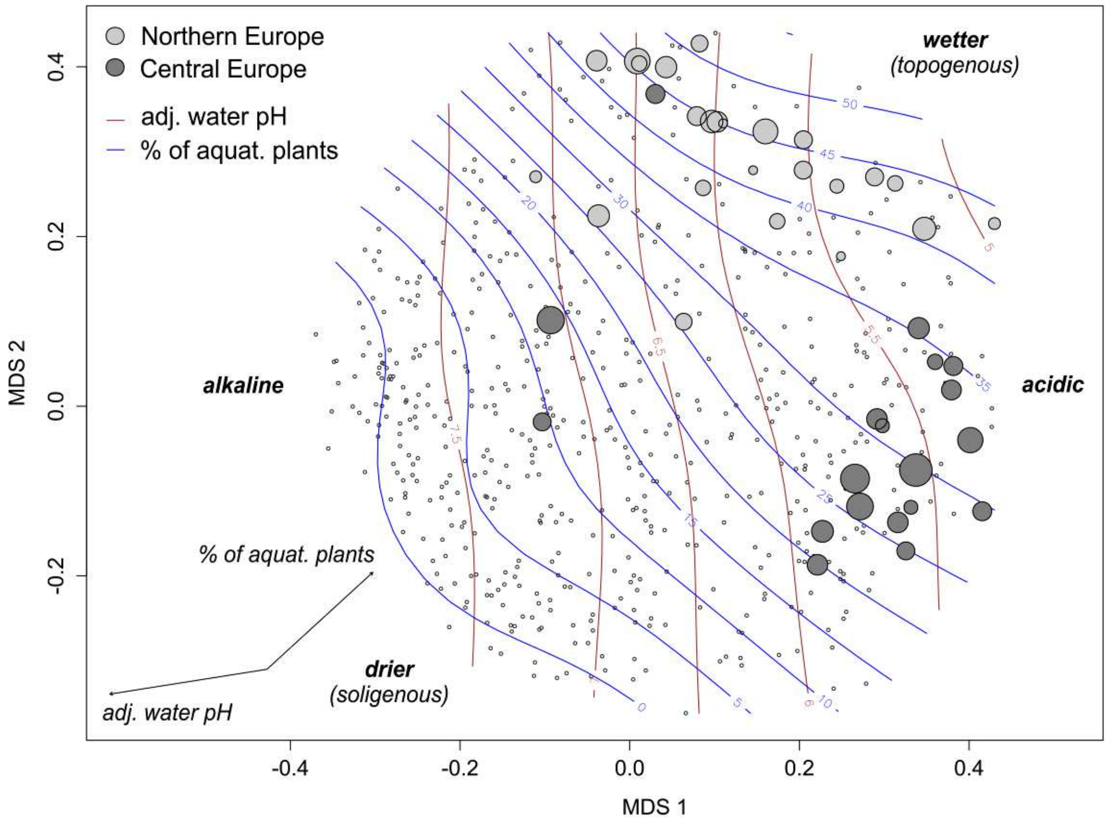

Figure 4. Position of 583 vegetation samples along the first two MDS axes based on plant composition variance. Samples with *Vertigo lilljeborgi* are given in full symbols, separately for Northern and Central Europe; the other samples are projected as small open circles. The size of full symbols matches the number of *V. lilljeborgi* individuals collected per 12-L sample volume (ln-transformed). Values of adjusted water pH and percentage cover of aquatic and semi-aquatic plant species at the sampling plots were plotted into the ordination space using smooth fitting.

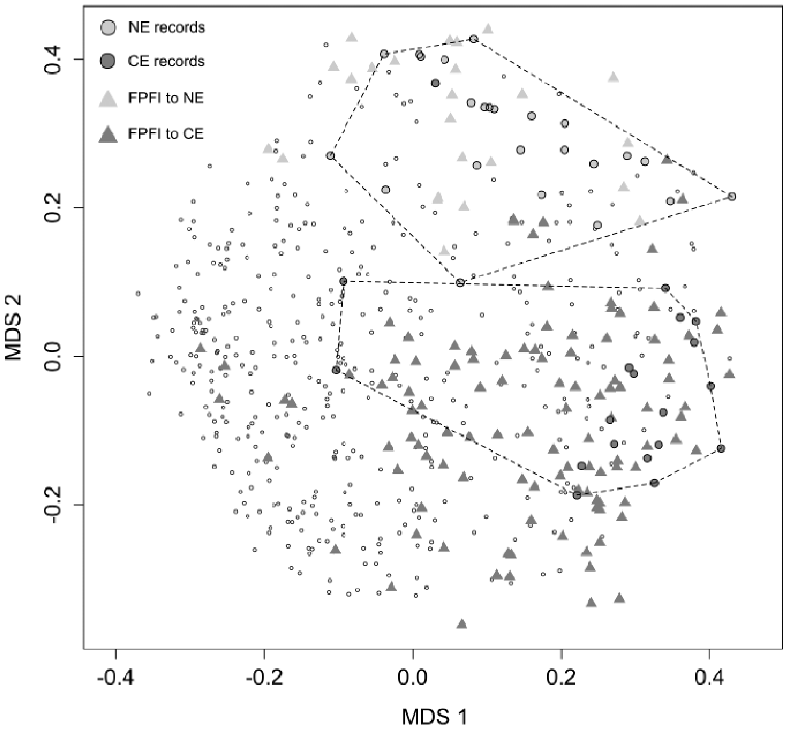

Figure 5. Position of 583 vegetation samples (relevés) along the first two MDS axes based on plant composition variance (the same analysis as for Fig. 3). Samples with *Vertigo lilljeborgi* are shown as full circles, separately for Northern Europe (NE) and Central Europe (CE). Full triangles are relevés from either Northern Europe (FPFI to NE) or Central Europe (FPFI to CE) with significant fidelity to the relevés with *V. lilljeborgi* either in Northern or Central Europe, respectively. Envelopes cover the samples with *V. lilljeborgi* (note that one outlier site from Central Europe was not included into the Central European cluster).

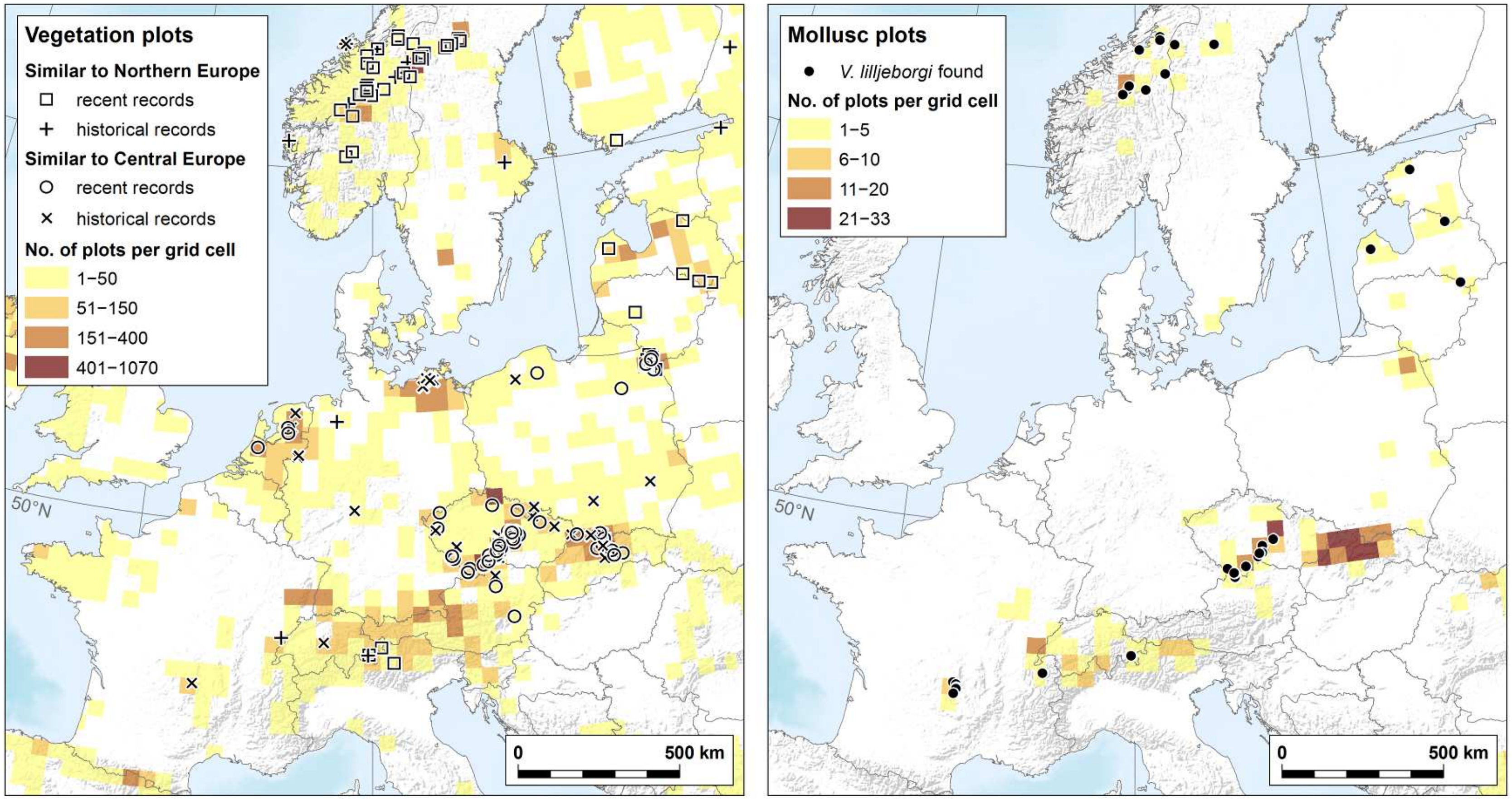

Figure 6. Right: Location of plots with favourable conditions for *Vertigo lilljeborgi* indicated by the similarity between vegetation of these plots and vegetation of either Northern (square and plus-sign) or Central (circle and cross) European sites containing it; categorized as recent (i.e. collected after 2000; square and circle) or historical (plus-sign and cross). Frequency of all mire vegetation plots used in the analysis is shown by using a colour-scale at 50 × 50 km UTM grid cells. Left: Distribution of *V. lilljeborgi* sites used in the ecological analysis (full dots). Frequency of 583 mire mollusc samples plotted at the same grid system is shown as for vegetation.

Table S1. List of all *Vertigo lilljeborgi* records from temperate mainland Europe, beyond its continuous distribution in Fennoscandia and the Baltic countries.

Latitude	Longitude	Country	Nearest town	Location	No. of inds	Year	Referrence / Collector (lgt.)
49°35'07.0"	15°56'32.0"	Czech Republic	Ždár nad Sázavou	Louky u Černého lesa NR	11	2012	M. Horsák lgt.
48°35'49.4"	14°13'40.9"	Czech Republic	Vyšší Brod	Rašeliniště Kapličky NR	9	2012	J. Hlaváč lgt.
48°36'10.1"	14°12'45.4"	Czech Republic	Vyšší Brod	Rašeliniště Kapličky NR	50	2012	J. Hlaváč lgt.
49°25'43.0"	15°27'00.0"	Czech Republic	Jihlava	U Šeredů, an acidic fen	3	2013	J. Myšák lgt.
49°13'60.0"	15°25'33.0"	Czech Republic	Telč	Doubský a Bažantka NR	7	2013	M. Horsák lgt.
49°07'54.0"	15°14'19.0"	Czech Republic	Strmilov	Rašeliniště u Suchdola NR	9	2013	M. Horsák lgt.
49°13'16.7"	15°18'35.9"	Czech Republic	Počátky	Zhejral NNM	8	2013	M. Horsák lgt.
48°52'43.0"	14°41'29.0"	Czech Republic	Borovany	Brouskův mlýn NNR	3	2014	M. Horsák lgt.
48°43'24.0"	14°10'45.0"	Czech Republic	Horní Planá	Lukavický potok Brook	22	2014	J. Hlaváč lgt.
49°41'54.1"	12°28'22.0"	Czech Republic	Rozvadov	Na Požárech NNM	9	2014	M. Horsák lgt.
48°51'01.8"	13°55'15.0"	Czech Republic	Volary	Vltavský luh NM	4	2015	M. Horsák lgt.
*49°12'51.0"	12°36'56.0"	Germany	Cham	Rötelsee Lake by Michelsdorf	?	1964	Hässlein (1964)
*47°48'10.0"	08°10'58.0"	Germany	Lenzkirch	Schluchsee Lake, south shore	2	1977, 1979	Gerber (1987)
*52°36'14.0"	13°17'36.0"	Germany	Hermsdorf-Berlin	Tegeler Fliess	?	?1921	Schmierer (1921)
46°29'21.0"	09°51'07.0"	Switzerland	St. Moritz	Mauntschas Mire	7	2012	Schenková & Horsák (2013)
45°30'50.4"	02°47'58.3"	France	Issoire	La Fontaine Salée Mire	9	2011, 2016	Vrignaud (2012); M. Horsák lgt.
45°28'12.0"	02°55'17.5"	France	Issoire	Lac de Bourdouze Lake	10	2016	M. Horsák lgt.
45°22'31.1"	02°56'41.0"	France	Issoire	Lac de Roche Orcine Lake	30	2010, 2016	Lecaplain (2013); M. Horsák lgt.
45°20'23.2"	02°56'16.8"	France	Massiac	Col de Chamaroux Spring	6	2016	M. Horsák lgt.
45°12'18.3"	02°50'55.4"	France	Massiac	Tourbiére du Jolan Mire	7	2016	M. Horsák lgt.
45°56'53.1"	06°19'09.0"	France	Annecy	Plateau des Glières	24	2013, 2016	E. Boyer lgt.; M. Horsák lgt.
45°03'16.5"	05°56'13.3"	France	Grenoble	Lac de la Vache Lake	9	2016	Combrisson & Vuinée (2017)
45°03'14.3"	05°56'04.7"	France	Grenoble	Lac de l'Agneau Lake	2	2016	Combrisson & Vuinée (2017)
*42°30'04.0"	02°02'27.0"	France	Prades	Font-Romeu	?	1928	van Regteren Altena (1934)
*42°25'01.0"	02°52'31.0"	Spain	Figueres	La Junquera	?	1960	von Proschwitz (2003)

* - geographical coordinates refer to more general areas than corresponding to their accuracy due to uncertainty of precise location of the original sampling sites

Table S2. List of land-snail species recorded in samples with *Vertigo lilljeborgi* from fen habitats across mainland Europe (N=43).

Land-snail species	**No. of sites**	**Rel. freq. (%)**
Euconulus praticola (Reinhardt, 1883)	30	71.4
Nesovitrea hammonis (Ström, 1765)	24	55.8
Succinea putris (Linné, 1758)	19	45.2
Vertigo substriata (Jeffreys, 1833)	16	38.1
Carychium minimum Müller, 1774	14	33.3
Punctum pygmaeum (Draparnaud, 1801)	14	33.3
Cochlicopa lubrica (Müller, 1774)	9	21.4
Deroceras laeve (Müller, 1774)	9	21.4
Vertigo antivertigo (Draparnaud, 1801)	8	19.0
Nesovitrea petronella (Pfeiffer, 1853)	7	16.7
Vertigo geyeri Lindholm, 1925	7	16.7
Zonitoides nitidus (Müller, 1774)	7	16.7
Oxyloma elegans (Risso, 1826)	5	11.9
Vertigo genesii (Gredler, 1856)	5	11.9
Vitrea crystallina (Müller, 1774)	5	11.9
Columella columella (v. Martens, 1830)	4	9.5
Eucobresia diaphana (Draparnaud, 1805)	4	9.5
Arianta arbustorum (Linné, 1758)	2	4.8
Arion fuscus (Müller, 1774)	2	4.8
Deroceras agreste (Linné, 1758)	2	4.8
Vallonia pulchella (Müller, 1774)	2	4.8
Arion ater (Linné, 1758)	1	2.4
Carychium tridentatum (Risso, 1826)	1	2.4
Cochlicopa nitens (Gallenstein, 1852)	1	2.4
Columella aspera Waldén, 1966	1	2.4
Euconulus fulvus (Müller, 1774)	1	2.4
Monachoides incarnatus (Müller, 1774)	1	2.4
Semilimax semilimax (Férussac, 1802)	1	2.4
Trochulus hispidus (Linné, 1758)	1	2.4
Vertigo arctica (Wallenberg, 1858)	1	2.4
Vertigo pygmaea (Draparnaud, 1801)	1	2.4
Vitrina pellucida (Müller, 1774)	1	2.4