ECOLOGICAL AND HISTORICAL DETERMINANTS OF WESTERN CARPATHIAN POPULATIONS OF *PUPILLA ALPICOLA* (CHARPENTIER, 1837) IN RELATION TO ITS PRESENT RANGE AND CONSERVATION

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ABSTRACT

The minute snail *Pupilla alpicola* (Stylommatophora: Pupillidae) is known as a threatened glacial relict restricted to treeless calcareous fens with Holocene continuity, mainly in the Alpine and Carpathian regions. We summarize all available data on the distribution of *P. alpicola* and analyse its ecological requirements in the Western Carpathians both at a larger, regional scale (162 sites) and at a smaller, within-site scale (10 sites). Viable populations of *Pupilla alpicola* occurred in 31 sites out of the 162 fens studied. Water conductivity, Ellenberg's indicator values for soil reaction, light and nutrients were the main ecological variables that explained these occurrences. The species preferred sites with extremely high calcium carbonate precipitation, low nutrients and sparse herb vegetation cover. Its present distribution in the Western Carpathians is strongly related to a spatial–temporal continuum of calcareous fens throughout the Holocene; none of the modern populations was located further than 40 km from the known palaeorefugium. Direct fossil evidence shows that these palaeorefugial fens have persisted since the Pleistocene/Holocene transition. A conservation strategy for this rare species needs to take account of both historical continuity and the maintenance of appropriate ecological conditions.

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INTRODUCTION

At the present time *Pupilla alpicola* (Charpentier, 1837) is a rare species limited to small and mostly isolated calcareous fen habitats scattered across the Alps (Klemm, 1974; Kerney, Cameron & Jungbluth, 1983; Falkner, 1998; Turner *et al.*, 1998; Gargominy & Ripken, 2006) and the Carpathians (Grossu, 1987; Lisický, 1991; Alexandrowicz, 1994; Horsák & Hájek, 2003; Horsák, 2005; Horsák & Cernohorsky, 2008; Horsák *et al.*, 2010a). Various ecomorphological types of the presumed *Pupilla alpicola* clade were more widespread during the central European full-glacial, probably due to the more widespread occurrence of suitable habitats (Ložek, 1964, 1992).

Pupilla alpicola requires treeless calcareous fens and in recent times only isolated populations in such habitats have been found (Klemm, 1974; Turner *et al.*, 1998; Horsák & Hájek, 2003; Pokryszko, 2004; Wiktor, 2004; Horsák *et al.*, 2007a). These habitats are characterized by extremely high mineral richness of their ground waters, which results in a strong calcium carbonate precipitation as tufa. While high calcium levels are generally favourable for land snails, most other species living in fens have lower optimum levels of mineral richness and wider environmental amplitudes than *P. alpicola* (Horsák, 2006).

Unlike a number of other wetland land snails (e.g. *Vertigo* species of European importance, cf. Vavrová *et al.*, 2009), *P. alpicola* does not receive any official European protection, despite figuring in the Red Lists of endangered species in every country where it occurs. The level of its protection in each depends on the number of its populations and the degree of habitat degradation in each country (Turner, Wüthrich & Rüetschi, 1994; Turner *et al.*, 1998; Falkner *et al.*, 2003; Pokryszko, 2004; Beran, Juřičková & Horsák, 2005; Šteffek & Vavrová, 2006). Its habitats are threatened by human-made impacts (e.g. aforestation, drainage for agriculture, acidification, nitrification, surface disturbances) and also natural processes such as spontaneous succession towards shrubby and forest habitats, mainly after the cessation of traditional management (Stanová, 2000; Horsák & Cernohorsky, 2008).

The primary aim of this study was to gain precise data on the conditions in which the species can maintain viable populations, and to examine the extent to which sites having these conditions were actually occupied. In addition we summarize data on the overall distribution and relate these to conservation strategy.

MATERIAL AND METHODS

Field sampling and explanatory variables

Samples were collected as part of a research project on all types of fens in the Western Carpathian region between 2001 and 2008 at 162 sites (Poulíčková, Hájek & Rybníček, 2005; Hájek *et al.*, 2011; M.H., unpubl.). Samples were collected at two different scales in order to study habitat requirements (large scale) and microhabitat preferences within a site (small scale). The sampling done to study habitat requirements consisted of collecting one 12-l sample of the upper fen layer from a 4 m × 4 m area in the central portion of each community ($n = 162$). Snails were extracted from samples using the 'wet sieving technique' (Horsák, 2003), in which material from each sample is gradually washed through a bowl-shaped sieve (mesh size 0.5 mm) to remove fine soil and coarse plant matter. After drying, shells were separated from the remaining material by hand-sorting under a stereo microscope and identified and counted, separating live individuals and empty shells. Live individuals of *Pupilla alpicola* were recorded in 31 sites; four other sites out of all 162 studied with only empty shells were

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Table 1. The list of ecological and geographical variables used to define ecological preferences of *Pupilla alpicola* in the Western Carpathians at both large (all variables) and small (marked by asterisk) scales. The values refer to the large scale.

	Mean	Std. Dev.
Refugium distance (km)	46	30
Latitude	49.16	0.22
Longitude	19.08	1.03
Altitude (m a.s.l.)	613	163
Mean January temperature (°C)	2.22	0.96
Mean July temperature (°C)	14.91	1.46
Mean annual temperature (°C)	5.13	1.50
Mean annual precipitation (mm)	937	199
Snow Cover (cm)	108	27
Water conductivity (μS/cm)*	391	199
Water pH*	6.99	0.66
Herb cover (%)	72.7	15.9
Moss cover (%)	81.5	18.4
Ellenberg's IV for light*	7.39	0.26
Ellenberg's IV for soil reaction*	6.36	0.91
Ellenberg's IV for temperature*	4.92	0.37
Ellenberg's IV for nutrients*	3.28	0.60
Ellenberg's IV for soil moisture*	7.74	0.47
Ellenberg's IV for continentality*	3.41	0.25

excluded from the large spatial-scale analyses. The sampling done to study microhabitat preferences covered 10 sites where *P. alpicola* occurred, where 31 samples were collected; for each sample a 25 cm × 25 cm plot was cut to just below ground level, using a sharp knife, and removed along with the herbaceous vegetation, mosses, litter and the upper soil layer. Snails were then extracted using the procedure described above (Horsák, 2003). Only live specimens were used in the analyses. They were found at 14 plots out of all 31 sampled. Altogether 80 individuals, on average nine per plot, were collected.

The following environmental parameters were compiled for each sampling plot (Table 1). To asses calcium content, water conductivity and pH were measured at the microsites best supplied by water in small shallow holes dug in the sampling plots, using portable instruments with automatic temperature compensation (CM 101 and PH 119, Snail Instruments, Beroun, Czech Republic). As water conductivity correlates well with the concentration of calcium ions in fens ($r = 0.9$–0.95; Sjörs & Gunnarsson, 2002; Hájek *et al*., 2005), it can be used as a reliable proxy of calcium concentration (Horsák, 2006). Mean annual rainfall, mean annual temperature, mean January temperature and mean July temperature were obtained by using overlays of plot locations with a digital elevation model and climatic maps, based on Miklós (2002) and Tolasz (2007), in the ArcGIS 8.3 program (ESRI, 2003). Values of light, temperature, moisture, soil reaction and nutrients were estimated using Ellenberg's plant indicator system (Ellenberg *et al*., 1992). A vegetation relevé was sampled in the same 16-m^2 (large spatial scale) or 625-cm^2 plot (small spatial scale) as molluscs. The occurrence and cover of species were recorded on the nine-grade Braun–Blanquet scale (van der Maarel, 1979) for both vascular plants and bryophytes. For each vegetation plot, we calculated the average Ellenberg indicator (IV) values using the JUICE program (Tichý, 2002). The average IV is a mean of available Ellenberg IVs of species recorded on a particular sampling plot (for more details see Horsák *et al*., 2007a). Geographical co-ordinates (obtained with GPS in the field) were used to calculate the distance of each site to the nearest known palaeorefugium, i.e. recent fen habitat which, based on fossil records and radiocarbon dating of bottom layer sediment (see Hájek *et al*., 2011), is known to have had a historical continuity of treeless fen communities since the Pleistocene/Holocene boundary.

Analyses of ecological requirements at both scales

To define ecological preferences of *P. alpicola* we used the 19 ecological and geographical variables of all 162 study sites for the large scale; eight ecological variables of 31 plots sampled in 10 sites where the species occurred were used for the analysis of small-scale distribution (Table 1). The principal component analysis (PCA) on the correlation matrix (centred and standardized) of all studied sites based on 16 environmental factors was calculated to isolate the main ecological variation among all study sites and the relations among individual variables. Three geographical variables were passively projected into the resulting diagram. Relationships among site scores on the first four PCA axes and explanatory variables were analysed using Spearman's rank correlations (r_S). To find significant differences between sites with and without *P. alpicola* two statistical tests were used: nonparametric Mann–Whitney *U*-test and nonparametric Kruskal–Wallis ANOVA with median χ^2 test. The responses of individual species abundances to the selected environmental factors at the large spatial scale were fitted with generalized additive models (GAM; Hastie & Tibshirani, 1990) using Poisson's distributions because there are no *a priori* reasons to assume that organisms' responses should follow symmetrical curves (Austin, 1976). The response of species often takes more complex shapes. Smooth term complexity was selected using the Akaike Information Criterion (AIC). This criterion attempts to measure model 'parsimony' using the number of model degrees of freedom (the lowest AIC value means the highest parsimony). All options were chosen based on the recommendations of Lepš & Šmilauer (2003: 124–139). The CANOCO 4.5 package (ter Braak & Šmilauer, 2002) was used for ordination techniques and GAM modelling; STATISTICA 7 (Hill & Lewicki, 2007) for all unidimensional analyses.

RESULTS

Distribution of Pupilla alpicola

The present distribution of *Pupilla alpicola* is clearly discontinuous, with two distributional centres located in two mountain systems, the Alps (both the Western and the Eastern Alps) and the Western Carpathians, where this snail is locally frequent (Fig. 1). The majority of sites are from Switzerland (Turner *et al*., 1998), Austria (Klemm, 1974), Slovakia (Lisický, 1991; Horsák, 2005; M.H., 2006–2010, unpubl.) and N Italy (Schröder, 1910; Ehrmann, 1933; Schrott, 1939; Alzona, 1971; Schrott & Kofler, 1972; M. Bodon, 1998–2003, unpubl.; Gavetti *et al*., 2008).

Only very few or single records come from France (Anonymous, 2005; Gargominy & Ripken, 2006), Poland (Alexandrowicz, 1994) and Romania – the Eastern Carpathians (Grossu, 1987). In Germany, sites in northwestern Bavaria, near Pegnitz (Hasslein, 1960), have been lost by habitat degradation (Falkner *et al*., 2003). Elsewhere in Germany there are only a few recent records of *P. alpicola* within the boundaries of Berchtesgaden National Park (Falkner, 1998). *P. alpicola* has also been repeatedly reported from the Czech Republic (e.g. Juřičková, Horsák & Beran, 2001; Horsák, 2005) but, after the revision of voucher material, it was concluded that all these records belong to *Pupilla pratensis* (Clessin, 1871) (Horsák *et al*., 2010a). There are also records of *P. alpicola* from the Korab Mountain in Albania (Soós, 1924; Dhora & Welter-Schultes, 1996; Dhora, 2009; Fehér & Eröss,

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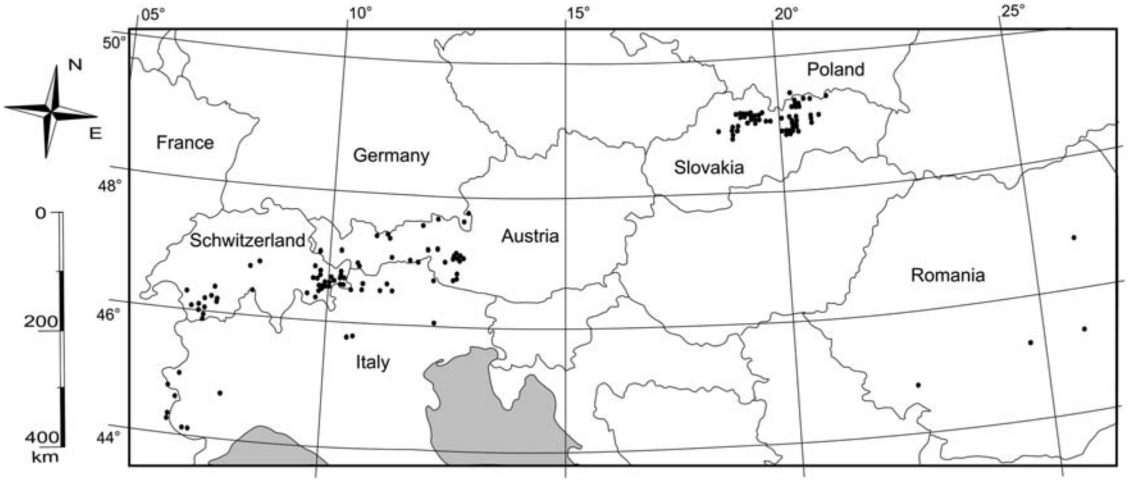

Figure 1. Modern distribution of *Pupilla alpicola* in Europe. For list of sources see Results.

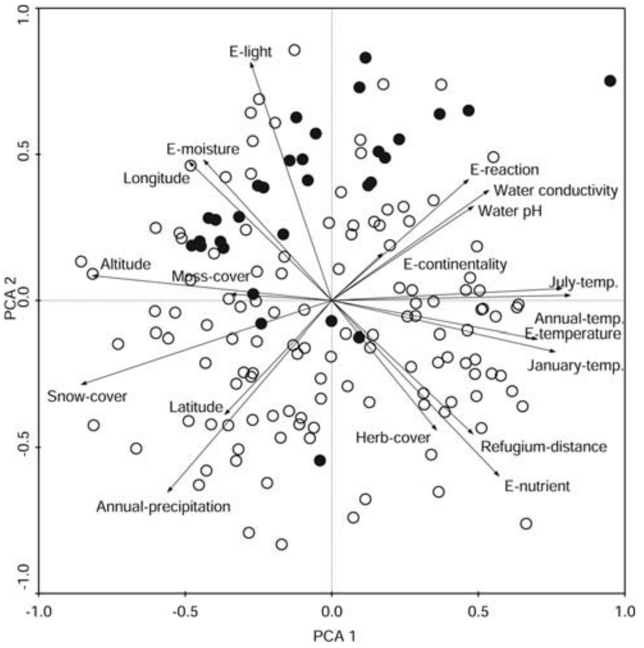

Figure 2. PCA ordination diagram of all the 162 study sites in Western Carpathians based on 19 explanatory variables (Table 1); sites ($n = 31$) with the presence of live *Pupilla alpicola* are marked by black dots. The first ordination axis explained 35.4% and the second 15.3% of total variation.

2009). Voucher material of the record published by Soós (1924) has been lost, but recent material collected from the same site in 2007 (leg. Z. Feher, det. M. Horsák) has confirmed that the original material was misidentified and that the population belongs to *P. sterrii* (Voith, 1840).

There is only one record of *P. alpicola* outside Europe, from southern Siberia (Altai Mts, Russia; Horsák *et al.*, 2010b) more than 4,000 km away from the nearest known site in eastern Romania. The species was abundant there; 24 live individuals and nine empty shells were found in a 12-l sample.

Large- and small-scale ecological requirements

The major environmental gradient (Fig. 2) within the set of explanatory variables, expressed by the first PCA axis, reflected the climatic differences, related mostly to elevation, and differences in mineral richness expressed by soil reaction and water conductivity (Table 2). However, the results of Kruskal–Wallis ANOVA did not show any strong significant differences between sites with and without *P. alpicola* population based on these variables (Table 3). In contrast, variables correlated with the second PCA axis, such as amount of nutrient and light condition, longitude and the distance to the nearest known palaeorefugial site (Table 2), were highly significant as explanatory factors for distinguishing between presence and absence of the species (Table 3). We found that sites inhabited by *P. alpicola* in the Western Carpathians were closer to the refugial fens ($P << 0.0001$, Mann–Whitney *U*-test) and were situated more eastwards. Extremely high mineral richness was the main ecological character of *P. alpicola* sites (based on water conductivity). These sites were also characterized by low plant productivity and a high proportion of light-demanding plant species (based on Ellenberg IVs for nutrients and light). The results of GAM models of species response curves confirmed these findings (Fig. 3).

At the smaller scale within a site the variation in moisture, amount of light and nutrients composed the major environmental gradient expressed by the first PCA axis. The mineral richness gradient, expressed as soil reaction and measured water pH, was correlated with the second PCA axis. However, quadrats with and without the species differed significantly only in Ellenberg's value for light ($P = 0.024$, Mann–Whitney *U*-test; $P = 0.023$, Kruskal–Wallis ANOVA); the species preferred sites with higher values which indicates lower cover by the vegetation canopy. None of the GAM models of the species response curve used were significant, but that for Ellenberg's value for light was nearly significant ($P = 0.076$).

DISCUSSION

Modern distribution

The distribution of *Pupilla alpicola* in Europe reflects both the distribution of suitable habitats and also the historical continuity of such habitats throughout the Holocene (Horsák *et al.*, 2007b; Hájek *et al.*, 2011). Thus, in the Western Carpathians *P. alpicola* occurs quite frequently in suitable habitats in the inner Western Carpathians, contrary to the outer Western Carpathians where the snail is missing despite a high frequency of sites with suitable habitats there (see Horsák *et al.*, 2007b). On the basis of fossil evidence it is known that some calcareous

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Table 2. The Spearman correlations between explanatory variables and site scores on the first four ordination axes ($P << 0.001$) of PCA that was based on the correlation matrix (centred and standardized) of all explanatory variables of the large spatial-scale data set.

Variables	PCA AX1	PCA AX2	PCA AX3	PCA AX4
Refugium distance	n.s.	−0.50	n.s.	n.s.
Latitude	n.s.	n.s.	n.s.	n.s.
Longitude	−0.54	0.47	n.s.	n.s.
Altitude	−0.84	n.s.	n.s.	n.s.
Mean January temperature	0.76	n.s.	n.s.	n.s.
Mean July temperature	0.78	n.s.	n.s.	n.s.
Mean annual temperature	0.82	n.s.	−0.46	n.s.
Mean annual precipitation	−0.54	−0.63	n.s.	n.s.
Snow Cover	−0.87	n.s.	n.s.	n.s.
Water conductivity	0.67	n.s.	n.s.	n.s.
Water pH	n.s.	n.s.	n.s.	−0.57
Herb cover	n.s.	−0.49	n.s.	n.s.
Moss cover	n.s.	n.s.	n.s.	n.s.
Ellenberg's IV for light	n.s.	0.81	n.s.	n.s.
Ellenberg's IV for soil reaction	−0.53	n.s.	n.s.	−0.49
Ellenberg's IV for temperature	0.76	n.s.	n.s.	n.s.
Ellenberg's IV for nutrients	0.54	−0.62	n.s.	n.s.
Ellenberg's IV for soil moisture	n.s.	0.51	n.s.	n.s.
Ellenberg's IV for continentality	n.s.	n.s.	n.s.	n.s.

fens of the inner Western Carpathians have spatial–temporal continuity throughout the Holocene. There are several sites which originated as open calcareous fens in the Late Glacial and have lasted in this treeless state until now (Hájek *et al.*, 2011). Four of these relictual fens (Hozelec, Močiar NNR, Valalská Voda NR and Štrba) have also been inhabited by *P. alpicola* continuously from the Late Glacial (M.H., unpubl.). The existence of these refugia, and the distance between them and other sites suitable for the species, is one of the most important factors shaping the present distribution of this species. The majority of known populations in Slovakia are situated in sites formed during mediaeval times by human-made deforestation where springs opened on calcareous bedrock (Horsák, 2005; Horsák *et al.*, 2007b; Hoffmann *et al.*, 2011). This study shows that these populations are not situated further than 40 km from the nearest glacial refugium ($P <<$ 0.001, Mann–Whitney *U*-test).

The first record of *P. alpicola* in central Asia emphasizes the present disjunct distribution as a relic of a distinctly wider distribution range of this species in the Last Glacial; southern Siberia is considered as the best modern analogy of central European landscape during the Last Glacial (Kuneš *et al.*, 2008; Meng, 2008; Horsák *et al.*, 2010b). The composition of co-occurring snail species at this Asian site (*Columella columella*, *Vertigo genesii*, *V. parcedentata* and *Vallonia tenuilabris*) clearly resembles assemblages known from the full-glacial loess sediments of central Europe (Ložek, 2000; Meng, 2008) and in this area *P. alpicola* represents a relic from the Last Glacial period.

Ecology of Pupilla alpicola *in the Western Carpathians – large and small spatial scale*

The strong ecological relation of *P. alpicola* to calcareous sites is well known (Ložek, 1982; Alexandrowicz, 1994; Turner *et al.*, 1998; Horsák & Hájek, 2003; Pokryszko, 2004; Wiktor, 2004; Horsák, 2006; Lang & Walentowski, 2007) and this habitat requirement results in a mosaic distribution of this species determined by the occurrence of this rare habitat type. Our results confirm a well-known fact that at the large spatial scale *P. alpicola* prefers sites with higher water conductivity – simply, it avoids calcium-poor sites (Ložek, 1982; Alexandrowicz, 1994; Turner *et al.*, 1998; Horsák & Hájek, 2003; Pokryszko, 2004; Wiktor, 2004; Horsák, 2006; Lang & Walentowski, 2007; Horsák *et al.*, 2007a). Only a few species such as *P. alpicola* are able to inhabit such extremely mineral-rich sites. It is one of few species which express a monotonic response curve, with the optimum in the extremely mineral-rich sites with strong tufa precipitation (Horsák, 2006). Fens inhabited by *P. alpicola* differed from the others by lower values of Ellenberg IV nutrients and higher values of Ellenberg IV light (Table 3, Fig. 3). Although these two variables create another ecological gradient, independent of the gradient in mineral richness (Fig. 2), the relation of *P. alpicola* to higher Ellenberg IV light and lower Ellenberg IV nutrient is also connected with the tufa precipitation. Precipitating tufa decreases the amount of available phosphorous which causes phosphorus-limited vegetation with lower density (Rozbrojová & Hájek, 2008) and such sparse vegetation allows for more light to reach the surface of the fen (Horsák *et al.*, 2007a).

Table 3. The Kruskal–Wallis ANOVA (*P*) and χ^2 median test (Chi-*P*) for groups of sites with and without *Pupilla alpicola* at the large spatial scale.

Kruskal–Wallis ANOVA	*P*	Chi-*P*
Refugium distance	<<0.001	<<0.001
Longitude	<<0.001	<<0.001
Ellenberg's IV for light	<<0.001	<<0.001
Ellenberg's IV for soil reaction	<<0.001	<0.01
Latitude	<0.001	<0.01
Ellenberg's IV for nutrients	<0.001	<0.02
Altitude	<0.01	<0.05
Ellenberg's IV for temperature	<0.01	<0.01
Herb cover	<0.02	<0.01
Mean January temperature	<0.01	<0.001
Mean annual precipitation	<0.02	n.s.
Water conductivity	<0.05	n.s.
Mean July temperature	<0.05	n.s.
Water pH	n.s.	n.s.
Mean annual temperature	n.s.	n.s.
Ellenberg's IV for soil moisture	n.s.	n.s.
Ellenberg's IV for continentality	n.s.	n.s.
Moss cover	n.s.	n.s.
Snow Cover	n.s.	n.s.
PCA AX1	n.s.	n.s.
PCA AX2	<<0.001	<<0.001
PCA AX3	<0.01	<0.05
PCA AX4	n.s.	n.s.

PCA AX1–4 represent site scores on the first four PCA axes.

Although it is known that fen biotopes can have variable spatial structures of ecologically different microhabitats (Horsák *et al.*, 2007a), very calcareous fens are rather uniform, mainly due to strong tufa precipitation that can cover the entire surface and decrease or unify structural niches (Horsák, 2006). This corresponds with our observations that none of the tested *P. alpicola* response models at the small spatial scale were significant, except the value of Ellenberg's light that significantly segregated plots with and without the species occurrence. This reflects small spatial variation of vegetation productivity directly visible on the

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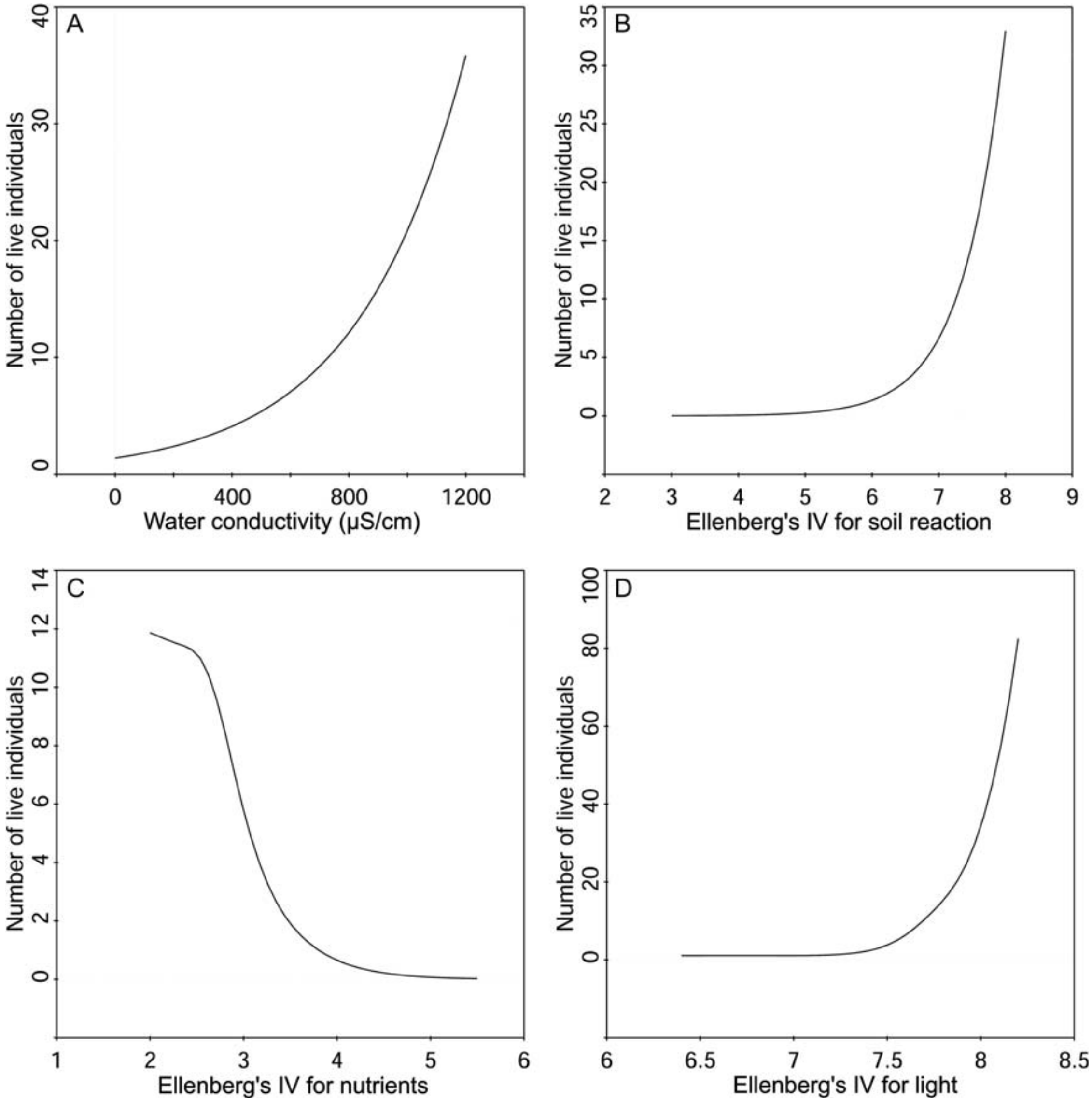

Figure 3. *Pupilla alpicola* response curves based on 31 populations in the Western Carpathians using GAM. **A.** Water conductivity, $P = 0.016$. **B.** Ellenberg's soil reaction, $P << 0.001$. **C.** Ellenberg's nutrients, $P < 0.001$. **D.** Ellenberg's light, $P << 0.001$.

basis of the presence of broad-leaved herbs in plots without *P. alpicola*.

Conservation implications

Our results show that while there are rather specific conditions in which *P. alpicola* can flourish, the existence of these conditions is a necessary but not a sufficient explanation for the present distribution. Historical continuity of suitable conditions is also important. The fact that suitable sites created by humans, but close to such refugial sites, have been colonized, albeit over centuries, suggests that there is a limited capacity for dispersal (see Horsák *et al.*, 2010c). There are present threats because calcareous fens are now mostly subject to successional changes towards more productive vegetation (Stanová, 2000), which is most often linked with the cessation of traditional farming of fens (Skeffington *et al.*, 2006). A long-term conservation strategy involves not only preventing such changes in sites holding the species, but also in others nearby that present suitable ecological conditions, allowing for natural colonization and the maintenance of a healthy metapopulation structure.

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