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Plant indicator values as a tool for land mollusc autecology assessment

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ABSTRACT

The aim of this paper was to utilize Ellenberg's plant indicator system for assessing mollusc autecology and to highlight possibilities and advantages of that approach in the case of fen mollusc communities. Molluscs and plants from 137 fen sites in the Western Carpathian Mountains were recorded quantitatively from homogeneous areas of 16 m^2. Water conductivity and pH were measured in the field. Values of Ellenberg's "light, temperature, continentality, moisture, soil reaction, and nutrients" were estimated for each site. The whole data set was processed using ordinations (PCA, DCA, and CCA) and generalized additive models (GAMs). We observed a strong correlation between water pH and Ellenberg soil reaction estimated by plant indicator values ($r = 0.72$, $P < 0.001$). Ellenberg soil reaction was found to be the best predictor of mollusc species composition, which expressed the main mineral-richness gradient. We found the existence of a second important gradient, the gradient of "light", expressing site and canopy openness. A tight correspondence between the results of species response curve modelling based on water conductivity and Ellenberg soil reaction confirmed that "soil reaction" does not express merely pH, but rather the total amount of calcium. We conclude that the Ellenberg's indicator system can be used to study the ecology of land molluscs, an important group of invertebrates in bioindication and nature conservation. Our data and approach could help design appropriate conservation management regimes for threatened snail species. We propose that our approach will be useful also in ecological studies of other animal groups.

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1. Introduction

One of the main goals of community ecology is to explain patterns of species composition and distributions. Several variables are responsible for these patterns and different species' ecological requirements play an important role, especially at smaller scales. The understanding of individual species ecology is important not only for the understanding of their within-the-range distribution but also for the prediction of species occurrences, and in the case of threatened species, for appropriate conservation scenarios and managements.

Land molluscs, especially snails, are an ecologically extraordinary group of animals due to the strong dependence on calcium as a major macronutrient constituent of their

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body (Dallinger et al., 2001). Molluscs need calcium for the growth of their shells (Wäreborn, 1970) and lack of calcium may also restrict their reproduction (Wäreborn, 1979). This relationship has been well studied on a community level and numerous authors have found a close relationship between the calcium content and the number of mollusc species and/or individuals (tens of papers, e.g. Wäreborn, 1970; Waldén, 1981; Pokryszko, 1993; Horsák and Hájek, 2003; Hylander et al., 2005). Unfortunately, the knowledge about individual species responses to single ecological factors is still lacking, except for calcium (Horsák, 2006) and our knowledge consists of fragmented data (despite many published papers, as cited above) or they concern only a few species (e.g. von Proschwitz, 1993; Speight et al., 2003; Horsák and Hájek, 2005). The second important environmental factor for land snails is soil moisture, however, fewer studies deal with this topic and most of them are without direct measurements (e.g. Wäreborn, 1969; Getz and Uetz, 1994; Martin and Sommer, 2004a,b). Unfortunately, little work has been done on the influence of other physical features of the habitat (e.g. Hermida et al., 1995; Barker and Mayhill, 1999; Nekola and Smith, 1999). Thus, we have a good understanding of land snail patterns in relation to gradients of calcium, but our knowledge of other aspects of their ecology is rudimentary.

There are probably two good reasons why the research on calcium has been dominant: (a) generally, the calcium content is the main control of snail community composition and structure, often significantly overtopping other environmental variables; and (b) it is an easily measurable factor, sometimes approximated by soil or litter pH, and it is also relatively temporary stable. Other environmental variables, in comparison, are not as easily measured. There are other difficulties, also, such as seasonal variation of environmental variables, which necessitate multiple repeated measurements, or technical problems associated with measurement of variable factors such as light, temperature, available nutrients or water regime on a large number of sites, especially if sites are far apart. Cost is also a factor. Therefore, inexpensive, flexible, and indirect methods of measuring these factors would be valuable. One potential approach is to use so-called plant indicator values to meet these requirements. In Central Europe, the ecological profiles of vascular plants are well known due to a long tradition of plant ecology, and due to the existence of large databases of species co-occurrences. Plant indicator systems can provide information about environmental factors quickly and easily on the basis of vegetation composition (Thomson et al., 1993; Ewald, 2003a). A recent and comprehensive system – Ellenberg's indicator values (Ellenberg et al., 1992) – provides tabular data about habitat requirements of nearly all Central European vascular plant species. By calculating the mean Ellenberg value of all plants recorded in a study site/plot we can obtain the position of a site/plot along particular ecological gradients. For these reasons the Ellenberg's system has enjoyed widespread application in plant ecology studies in Europe (e.g. Hill and Carey, 1997; Chytrý et al., 2003; Diekmann, 2003; and many others). The use of such plant indicator value systems in the study of animal autecology is in its infancy, but there have been some studies, e.g. butterflies (Oostermeijer and van Swaay, 1998; Konvička et al., 2003).

The aim of this study is to utilize the information contained in Ellenberg IVs in order to obtain new knowledge about the ecology of land molluscs, especially those inhabiting fens. We had five primary objectives: (1) to examine the possibility of using plant IVs for assessing autecology of molluscs inhabiting fens, (2) to test the validity of that approach on the basis of concordances between measured water pH and values obtained indirectly from plant IVs, (3) to study the interactions between other variables (light, temperature, continentality, moisture, soil reaction, and nutrients) and to highlight the main ecological gradients with respect to mollusc communities, (4) to explore which variable is the best predictor of mollusc community composition, and (5) to highlight possible utilization of plant indicator systems in studies of animal ecology.

2. Materials and methods

2.1. *Study area and study sites*

The study of 137 spring fen sites was carried out in the Western Carpathian Mountains of Central and Eastern Europe. The overall extent of study area was 12 000 km^2 (Fig. 1). The study area consists of two principal regions differing in their geology and historical development. The first one – the western region – includes the borderland between the Czech Republic and Slovakia and the Orava region in northern Slovakia. It is composed of flysch – a bedrock with sandstone and claystone alternating in each geological stratum (bed). The beds differ from each other both in chemistry and proportion of sandstone and claystone. The second one – the eastern region – is the northwestern part of the Inner Western Carpathians, which typically contains cores of Palaeozoic and crystalline schists overlaid by Mesozoic shale–sandstone and carbonate lithofacies (limestone and dolomite). The chemical composition of groundwater reflects the rock chemistry (Rapant et al., 1996). The overall chemical composition and climatic features do not differ between the regions (Hájek and Hekera, 2005; Hájek et al., 2005). The study sites were treeless sloping spring fens, which covered the entire variability of fens along the mineral poor–rich gradient (Malmer, 1986; Hájek et al., 2006). The six following vegetation types represent the most common fen habitats (arranged from mineral-richest to mineral-poorest): (1) Inner-Carpathian travertine swards (*Glauco-Trichophoretum pumili* association), (2) extremely mineral-rich tufa-forming fens (*Carici flavae-Cratoneuretum* ass.), (3) Inner-Carpathian calcareous peat-forming fens (*Caricetum davallianae* ass.), (4) Outer-Carpathian extremely rich peat-forming fens (*Valeriano simplicifoliae-Caricetum flavae* ass.), (5) moderately calcium-rich *Sphagnum*-fens (*Sphagno warnstorfii-Tomenthypnion* alliance), and (6) poor acid *Sphagnum*-fens (*Sphagno recurvi-Caricion canescentis* all.). For species composition of the above-mentioned vegetation types see Valachovič (2001) and Hájek et al. (2005).

2.2. *Field sampling and data collection*

Field work was conducted from 2000 to 2004. In each site, one sample of 12 l volume comprising the upper soil layer

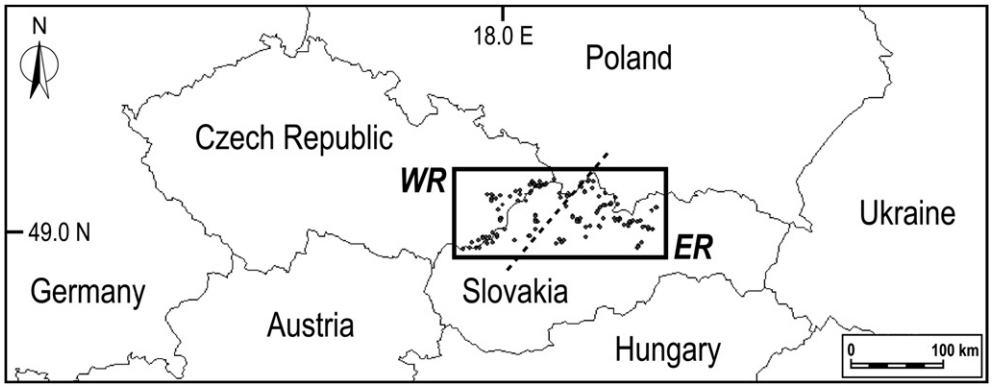


Fig. 1 – The position of all 137 sampling sites. Dashed line, border between two principal geographical regions: western (WR) and eastern (ER).

including litter, bryophytes, and herbaceous vegetation was collected in order to sample snail assemblages. The method of sample processing is described in detail by Horsák (2003). Samples were not collected randomly, as the material collected was meant to reflect the area (16 m^2), homogeneous in terms of vegetation composition and structure, in the central part of the site. The primary goal was always to detect the site's species as exhaustively as possible. Mollusc species names are given according to Juřičková et al. (2001), except *Euconulus alderi* (Gray, 1840), for which the name *Euconulus praticola* (Reinhardt, 1883) is used (Falkner et al., 2002). The species composition of the vascular plants was recorded in the same 16 m^2 (4 × 4 m) plots. The cover of each plant species was estimated using the Braun-Blanquet 9-grade scale (van der Maarel, 1979).

Water conductivity and pH were measured in the microsites best supplied by water in small shallow holes dug in the central part of the spring fen (inside the sampling plot), using portable instruments with automatic temperature compensation (CM 101 and PH 119, Snail Instruments, Beroun, Czech Republic). The readings were standardized to 20 °C. Conductivity was measured to indirectly approximate water mineral richness, especially Ca + Mg concentration (cf. Sjörs and Gunnarsson, 2002; Hájek et al., 2005) and conductivity caused by H^+ ions in acid waters was subtracted (Sjörs, 1952).

2.3. *About Ellenberg's plant indicator system and estimating explanatory variables*

Ellenberg's system is a typical expert system because the IVs were mostly assigned using Ellenberg's and others' knowledge of the environmental conditions that particular plant species prefer. Each of 2726 Central European vascular plant species was assigned to an ordinal numbers (e.g. IVs) designating its preference for position along particular ecological gradients (i.e. light, temperature, continentality, moisture, soil reaction, and nutrients), using a 12-point scale for moisture and a 9-point scale for the others (Ellenberg et al., 1992). Sites can be positioned on each gradient by (weighted) averaging of IVs of recorded plant species, because with a sample size of more than 100 species the indicator values tend to behave as continuous variables (ter Braak and Barendregt, 1986).

For each vegetation plot, we calculated the average Ellenberg IVs for ''light, temperature, continentality, moisture, soil reaction, and nutrients'' using the JUICE program (Tichý, 2002). The average IV is a mean of available Ellenberg IVs of species recorded on a particular sampling plot. A total of 293 vascular plant species were recorded in all studied plots, of which 234 (80%) had IV for light, 88 (30%) for temperature, 188 (64%) for continentality, 202 (69%) for moisture, 149 (51%) for soil reaction, and 214 (73%) for nutrients. Ewald (2003a) found the calculation of the mean value resilient to incompleteness of a vegetation relevé and thus to missing IVs of some recorded species.

When calculating Ellenberg IVs, the uneven number of species assigned to different indicator values by Ellenberg et al. (1992) can bias the results as pointed out by Schaffers and Sýkora (2000). They proposed the method of negative weighting by the number of species assigned to particular values on Ellenberg scale. Nevertheless, on the basis of our experience and pilot analyses, the weighted and unweighted averages gave roughly similar results (see also Chytrý et al., 2003). We have therefore used unweighted averages.

2.4. *Interpretation of factors evolved from plant indicator values*

In order to understand the patterns revealed by this study correctly we have to explain the real ecological meaning of the variables calculated from Ellenberg IVs. The value given for each sample is calculated through its total species composition of vascular plants. The increasing value of some factor is therefore caused not only by increasing the number of plant species preferring one end of the gradient, but also by the absence of the species from the opposite end of the gradient. Moreover, direct comparison of Ellenberg IVs with measured data (Schaffers and Sýkora, 2000) has shown that the name of an Ellenberg factor does not always reflect its real content clearly. The increasing value of Ellenberg's factor ''*nutrients*'', which refer not only to nitrogen but to all three major nutrients, must be therefore interpreted as increasing representation of nutrient-demanding plant species, i.e. meadow forbs and grasses in the case of fen habitats. There is a general lack of correlation between soil nutrient concentrations and

Ellenberg value for "nutrients" and this value strongly correlates with plants' biomass production (Schaffers and Sýkora, 2000). Molluscs can respond to this gradient because of better palatability of forbs and grasses and their litter when compared with sedges and/or altered micro-climatic conditions underneath high amount of biomass and litter accumulation. The increasing value of Ellenberg's "*light*" indicates decreasing representation of species characteristic of forests and shrubs and/or decreasing density of vegetation canopy allowing penetration of photosynthetically active radiation to lower vegetation layers (Kotowski et al., 2001). The increasing value of Ellenberg's factor "*soil reaction*" does not express merely pH, but rather the total amount of calcium at higher pH values (Schaffers and Sýkora, 2000). Ellenberg's "*moisture*" expresses mostly average lowest moisture contents in summer, but it correlates also with the annual average groundwater level and the average spring level (Schaffers and Sýkora, 2000). In the case of at least moderately calcareous spring fens, which support the occurrence of molluscs, this gradient is very short as water level rarely goes below −30 cm. However, even a small seasonal decrease causes desiccation of the fen surface especially in the tufa-forming fens (Hájková et al., 2004). Molluscs inhabiting fens with low Ellenberg values for moisture are still wetland species, but they are adapted to seasonal desiccation of the fen surface.

2.5. *Statistical analyses*

The mollusc samples subjected to ordination were based on live specimens and empty shells with entire periostracum. Only species which occurred in >9 sites were taken into account (altogether 40 species; 2010 records; and 89 207 specimens), and their abundances were log-transformed as $Y = \log(n + 1)$. For full species name see Table 1. For the species response curve modelling, only live specimens were taken into account and those recorded in >9 sites were analysed (altogether 32 species; 1460 records; and 51 136 specimens).

Since explanatory variables had uniform (moisture) or normal (the others) distribution (Kolmogorov–Smirnov test, cut level = 0.05), no transformation was made. The samples were ordinated on the basis of mollusc species composition using the partial canonical correspondence analysis (partial CCA) with geographical position (categorical, i.e. site was located in western or eastern region) as a co-variable. It was necessary to remove the variability explained by this factor because there are differences between mollusc communities of the western and eastern regions (Horsák et al., 2007). Moreover, we found that the differences in species composition between the two principal regions (Fig. 1) are caused exclusively by historical events and they do not match with any environmental variable (Hájek et al., 2005; Horsák et al., 2007).

From the explanatory variables, a subset of significant predictors was selected using the Monte Carlo permutation test with forward selection procedures (for details see Lepš and Šmilauer, 2003: 41, 64). The number of permutations was arbitrarily assigned to 999. This test evaluated the power of particular explanatory variables, thus only significant ones were illustrated in the ordination biplot (ter Braak and Šmilauer, 2002).

Individual species responses to target factors were modelled with a generalized additive model (GAM, Hastie and Tibshirani, 1990) using the Poisson distribution. The GAMs were used because usually there are no *a priori* reasons to assume that an organism's 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 (lowest AIC value = highest parsimony). All options were chosen based on the recommendations of Lepš and Šmilauer (2003: 124–139). The obtained response curves were divided into five categories: a monotonic decreasing – Mon(−); a unimodal with optimum skewed to the lower values – Uni(−); a unimodal with optimum around the centre – Uni(0); a unimodal with optimum skewed to the higher values – Uni(+); and a monotonic increasing – Mon(+) (Fig. 2). The CANOCO 4.5 package (ter Braak and Šmilauer, 2002) was used for all ordination techniques and for GAM modelling. STATISTICA 7 (www.statsoft.com) was used for the other (uni-dimensional) analyses.

Table 1 – The list of analysed mollusc species

Full name	Abbreviation
Bythinella austriaca s.lat. (von Frauenfeld, 1857)	BytAus
Platyla polita (Hartmann, 1840)	PlaPol
Galba truncatula (O.F. Müller, 1774)	GalTru
Radix peregra (O.F. Müller, 1774)	RadPer
Anisus leucostoma (Millet, 1813)	AniLeu
Carychium minimum (O.F. Müller, 1774)	CarMin
Carychium tridentatum (Risso, 1826)	CarTri
Cochlicopa lubrica (O.F. Müller, 1774)	CocLub
Pupilla alpicola (Charpentier, 1837)	PupAlp
Vallonia costata (O.F. Müller, 1774)	ValCos
Vallonia pulchella (O.F. Müller, 1774)	ValPul
Acanthinula aculeata (O.F. Müller, 1774)	AcaAcu
Columella edentula (Draparnaud, 1805)	ColEdu
Vertigo angustior (Jeffreys, 1830)	VerAng
Vertigo antivertigo (Draparnaud, 1801)	VerAnt
Vertigo geyeri (Lindholm, 1925)	VerGey
Vertigo pygmaea (Draparnaud, 1801)	VerPyg
Vertigo moulinsiana (Dupuy, 1849)	VerMou
Vertigo substriata (Jeffreys, 1833)	VerSub
Succinella oblonga (Draparnaud, 1801)	SucObl
Succinea putris (Linné, 1758)	SucPut
Oxyloma elegans (Risso, 1826)	OxyEle
Punctum pygmaeum (Draparnaud, 1801)	PunPyg
Zonitoides nitidus (O.F. Müller, 1774)	ZonNit
Euconulus praticola (Reinhardt, 1883)	EucPra
Euconulus fulvus (O.F. Müller, 1774)	EucFul
Vitrina pellucida (O.F. Müller, 1774)	VitPel
Vitrea diaphana (Studer, 1820)	VitDia
Vitrea crystallina (O.F. Müller, 1774)	VitCry
Aegopinella pura (Alder, 1830)	AegPur
Perpolita hammonis (Strőm, 1765)	PerHam
Perpolita petronella (L. Pfeiffer, 1853)	PerPet
Daudebardia rufa (Draparnaud, 1805)	DauRuf
Deroceras laeve (O.F. Müller, 1774)	DerLae
Fruticicola fruticum (O.F. Müller, 1774)	FruFru
Plicuteria lubomirskii (Ślósarskii, 1881)	PliLub
Perforatella bidentata (Gmelin, 1791)	PerBid
Monachoides incarnatus (O.F. Müller, 1774)	MonInc
Pisidium casertanum (Poli, 1791)	PisCas
Pisidium personatum (Malm, 1855)	PisPer

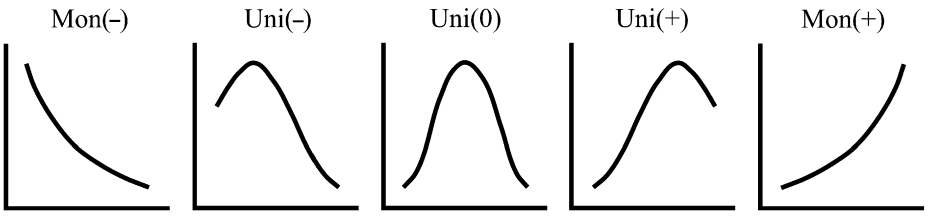


Fig. 2 – The distinguished five categories of species response curves: a monotonic decreasing – Mon(−); a unimodal with optimum skewed to the lower values – Uni(−); a unimodal with optimum around the centre – Uni(0); a unimodal with optimum skewed to the higher values – Uni(+); and a monotonic increasing – Mon(+).

3. Results

3.1. *Correlation between variables and environmental gradients*

The highest value of Pearson correlation coefficient "*r*" (Table 2) was observed between water pH measured in the field and soil reaction estimated by plant IVs ($r = 0.72$, $P < 0.001$). A similar, but negative, correlation was obtained for Ellenberg IVs for light and nutrients ($r = -0.69$, $P < 0.001$). Higher correlation values were also observed between nutrients and moisture ($r = -0.57$, $P < 0.001$) as well as between nutrients and temperature ($r = 0.51$, $P < 0.001$). Remaining variables showed weak or not significant correlations (Table 2).

The first PCA axis accounted for 62.7% of the variance of the correlation matrix. High loadings on this axis, reflecting correlations with the sample scores, were obtained for soil reaction ($r = -0.96$, $P < 0.001$) and pH measured in the field ($r = -0.85$, $P < 0.001$). The first axis thus represented the base-richness gradient (Table 3). The second axis accounted for 19% of the variance of the correlation matrix. The higher loadings were obtained for all remaining variables but continentality (Table 3). The second axis expressed an important, but, complex gradient (see Table 3). The third and fourth axes accounted only for minor part of the variability and they reflected residual variance in single variables (for summary of results see Table 3).

3.2. *Species–environment relationship*

Species composition of fen mollusc communities was governed by two ecological gradients (Table 4). The first partial DCA axis was controlled by a gradient of base-richness; the higher loading was obtained for the soil reaction ($r = -0.74$, $P < 0.001$). The most calcicole species were displayed on the left hand side of the ordination diagram, compared with the right hand side, with the most calcifuge ones. The second axis expressed the gradient of site and canopy openness; the higher loading was obtained for "light" ($r = 0.37$, $P < 0.001$). The species of largely open sites with a sparse vegetation cover (e.g. *Pupilla alpicola*) were placed on the upper part, contrary to the lower part with an assemblage of all species preferring forest habitats (e.g. *Daudebardia rufa*). Other variables contributed to both gradients (Table 4).

The soil reaction was the best predictor of species composition, which accounted for >43% of explained variation in CCA (Table 5). From the variables composing the second ecological gradient (Table 3, the second axis), species composition showed the greatest response to the "light" (Table 5). The distribution of both the species and the variables in the partial DCA and partial CCA diagrams was in high correspondence (Table 4 and Fig. 3). This result confirmed the existence of the two above-mentioned principal gradients, which accounted for most of the variation in species composition of the studied sites.

3.3. *Species optima and species response curve*

The positions of individual species optima along each environmental gradient are shown in Fig. 4. A high correlation between positions of species optima for soil reaction and water pH was obtained ($r = 0.92$, $P < 0.001$; see Fig. 4). There was an uneven distribution of the species optima positions on the ordination axes (Fig. 4), except for temperature, which was realized on a smaller scale. For all factors, the majority of species

Table 2 – Correlation between explanatory variables: Pearson correlation coefficients (lower left) and their significance probabilities (upper right), $n = 137$

	Water pH	Soil reaction	Light	Temperature	Continentality	Moisture	Nutrients
Water pH		<0.001	–	<0.025	–	<0.001	<0.001
Soil reaction	0.72		–	–	–	<0.001	<0.0025
Light	−0.06	0.13		<0.001	–	<0.001	<0.001
Temperature	0.22	0.17	−0.35		–	<0.001	<0.001
Continentality	0.00	0.04	−0.01	−0.08		–	–
Moisture	−0.31	−0.32	0.53	−0.45	0.13		<0.001
Nutrients	0.34	0.28	−0.69	0.51	0.10	−0.57	

Not significant correlations are in italics. Water pH was measured directly in the field, the others were estimated using Ellenberg IVs.

Table 3 – PCA of seven explanatory variables in the 137 fen sites

PCA axis	1		2		3		4	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Eigenvalues	0.627		0.190		0.079		0.045	
Water pH	−0.85	<0.001	0.01	–	−0.52	<0.001	−0.03	–
Soil reaction	−0.96	<0.001	−0.20	<0.05	0.19	<0.05	0.02	–
Light	0.04	–	−0.84	<0.001	0.03	–	−0.00	–
Temperature	−0.28	<0.001	0.56	<0.001	0.04	–	−0.24	<0.01
Continentality	−0.03	–	0.01	–	0.06	–	0.48	<0.001
Moisture	0.44	<0.001	−0.61	<0.001	−0.18	<0.05	0.58	<0.001
Nutrients	−0.44	<0.001	0.84	<0.001	0.08	–	0.28	<0.001

Eigenvalues of axes, correlations of explanatory variables with the first four PCA axes (*r*) and their significance (*P*) are shown.

had their optima around zero and the majority of them expressed a wider ecological valence (i.e. their fit was relatively low).

For 28 out of 32 species for which we calculated species response curves, we observed 73 significant associations with Ellenberg IVs (Table 6). For soil reaction, 14 unimodal and 6 monotonic regressions were found. The majority of species displayed their optima at the alkaline end of the gradient. Similar ratios of unimodal and monotonic regressions were also observed for temperature (10/2) and nutrients (8/5). Almost all species can be considered as thermophilous. The presence of all species response types was found for ''nutrients''. We observed species highly abundant in nutrient-rich sites (e.g. *Pisidium personatum*) as well as threatened snails requiring oligotrophic habitats (e.g. *Vertigo geyeri*). The soil moisture expresses identical numbers of both regression types (6/6). Most species showed an association with well water-soaked habitats with stable water regime, but some molluscs tolerating seasonal water level decrease appeared as well. The dominance of monotonic regression was obtained for light and continentality, where any ecological explanation of our results was hard to find. In terms of response to light, species belong to two principal groups. The first group included species requiring largely open fens with sparse vegetation and the second one included species mostly occurring in small fens neighbouring the shrub and forest habitats.

4. Discussion

4.1. *Correlation between Ellenberg IVs and environmental variables*

Our results confirmed a close and significant correlation between water pH measured in the field and the estimated value of soil reaction. Moreover, the soil reaction was the best predictor of species composition. There are several reasons why estimated variables gave better results. First, Schaffers and Sýkora (2000) concluded that a site's mean soil reaction value accurately described the total amount of calcium in the soil, i.e. both exchangeable Ca^{2+} as well calcium in the form of carbonates. We obtained a higher correlation between water conductivity and soil reaction ($r = 0.61$, $P < 0.001$) than between water conductivity and water pH ($r = 0.54$, $P < 0.001$). As water conductivity correlates well with the concentration of calcium ions ($r = 0.9–0.95$; Sjörs and Gunnarsson, 2002; Hájek et al., 2005), it can be used as a reliable indicator of calcium concentration (Horsák, 2006). Additionally, Sjörs and Gunnarsson (2002) showed a strong linear correlation between conductivity and calcium concentration in mire water, when pH values are above 4.7 (which was the case for almost all our studied sites). So, we can accordingly conclude that mean soil reaction is a better proxy variable for calcium concentration than water pH. Given the need for calcium for molluscan shell growth

Table 4 – Correlations among explanatory variables and partial DCA ordination site scores on the three first ordination axes

pDCA axis	1		2		3	
	r	*P*	*r*	*P*	*r*	*P*
Water pH	−0.61	<0.001	0.21	<0.05	−0.13	–
Soil reaction	−0.74	<0.001	0.19	<0.05	−0.13	–
Light	−0.07	–	0.37	<0.001	0.16	–
Temperature	−0.16	–	0.23	<0.01	−0.14	–
Continentality	−0.13	–	0.11	–	0.03	–
Moisture	0.30	<0.001	0.08	–	0.00	–
Nutrients	−0.19	<0.05	−0.15	–	−0.13	–

Values of Pearson correlation coefficient (*r*) and significance probabilities (*P*) are shown.

Table 5 – The result of stepwise selection of the explanatory variables using forward selection in partial canonical correspondence analysis (pCCA)

Variable	Lambda	%	P-value	F-ratio
Soil reaction	0.132	43.1	0.001	8.520
Light	0.057	18.6	0.002	3.666
Temperature	0.032	10.5	0.001	2.071
Moisture	0.030	9.8	0.007	1.991
Continentality	0.028	9.2	0.016	1.855
Nutrients	0.026	8.5	0.026	1.700
Water pH	0.014	4.6	0.595	0.908

Lambda value, percentage of explained variation, P-value and F-ratio are given for each analysed variable.

(Wäreborn, 1970) and for other physiological processes (Wäreborn, 1979), this relationship is as expected. Furthermore, calcium content is the main ecological factor predicting qualitative and quantitative features of fen mollusc communities (Horsák and Hájek, 2003). In a previous study we found no correlation between water pH and mineral-richness in base-rich sites, which was caused mainly by HCO_3^- ion buffering, photosynthesis of plants, and water movement (for details see Horsák, 2006; 104). Consequently, in some of the most base-rich sites the relationship between water pH and calcium concentration is rather weak. Therefore, the power of the Ellenberg soil reaction IV to act as a proxy for calcium concentration/content has a wider ecological importance for studying land snail ecology.

4.2. *The main ecological gradients*

The mineral poor–mineral rich gradient (Malmer, 1986) is the main ecological gradient of mire habitats, which governs species composition of algae, bryophytes, vegetation, molluscs (e.g. Tahvanainen, 2004; Poulíčková et al., 2005), and probably

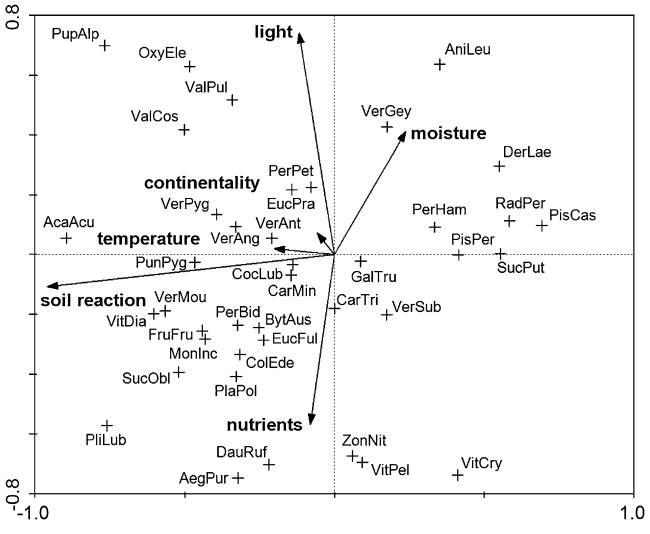


Fig. 3 – Partial CCA diagram of mollusc species on the first two canonical axes (geographical position as a co-variable). Eigenvalues: first axis 0.144, second axis 0.064. For the full species name see Table 1.

also other biota. On the other hand, there are also other gradients, which can be overtopped by the mineral poor–rich gradient, and consequently be missed or misinterpreted. For example, the correlation between IVs for soil reaction and nutrients (Table 2) is based on an older opinion that nitrogen availability increases in the richer fens. However, this opinion has been refuted by many recent papers (e.g. Wheeler and Proctor, 2000; Hájek et al., 2002).

By using Ellenberg IVs we detected other environmental gradients, for example the second important factor controlling fen mollusc distribution, a gradient of ''light'' (Fig. 3, the second axis), which is independent of the poor–rich gradient (Tables 3 and 4). The ecological interpretation of Ellenberg's ''light'' relates to the site's openness and density of vegetation layer (see Section 2.4). The complex factor ''light'', which is related mainly to total site area, distance from forest, and density of vegetation layer, can be closely related to different historical developments of fen sites situated in the eastern and western regions of study area (Fig. 1; for details see Horsák et al., 2007). Nevertheless, the ''light gradient'' also seems to have an ecological interpretation. Our field experience shows the relation of glacial relic *P. alpicola* to a sparse vegetation cover.

4.3. *Species autecology and species response curves: concordance with known data*

In general, the results are in a good concordance with previously published empirical data concerning individual mollusc species autecology (e.g. Ložek, 1956; Kerney et al., 1983; Cameron, 2003). More exact information about species responses to single variables are very unsatisfactory except for calcium. Therefore, we can judge the validity of IVs only on the basis of known calcium demands. Statistically, we were able to evaluate species preferences along the gradients of water pH/conductivity (directly measured) and soil reaction (estimated from IVs). As these variables express the main ecological gradient of the studied habitats, the evidence for their strong positive correlation is of high importance (see Fig. 4 and Table 4). We also obtained fairly high correspondence between species response curves modelled on the basis of Ellenberg soil reaction and water conductivity, which was used as a proxy of calcium concentration (Horsák, 2006). In 10 out of 15 species that had significant regressions in both approaches, the same type of response curve was observed. The five others had their optima shifted to more alkaline sites in the IV case, but in most cases merely from Uni(0) to Uni(+) (Fig. 2). These slight differences could be a consequence of an uneven distribution of the indicator values for the given species pool, as documented by Schaffers and Sýkora (2000) and Ewald (2003b). Also in our data set, a very large pool of species with indicator values of 7 and 8 was observed. Site mean IVs may be affected by this uneven distribution and consequently shifted, in the case of soil reaction, to higher values. This minor difference does not have any major effect on ecological interpretation.

Unfortunately, other exact autecological data concerning different environmental variables are known only for particular species – the threatened ones, for example *Vertigo moulinsiana*. Tattersfield and McInnes (2003) found that local density of

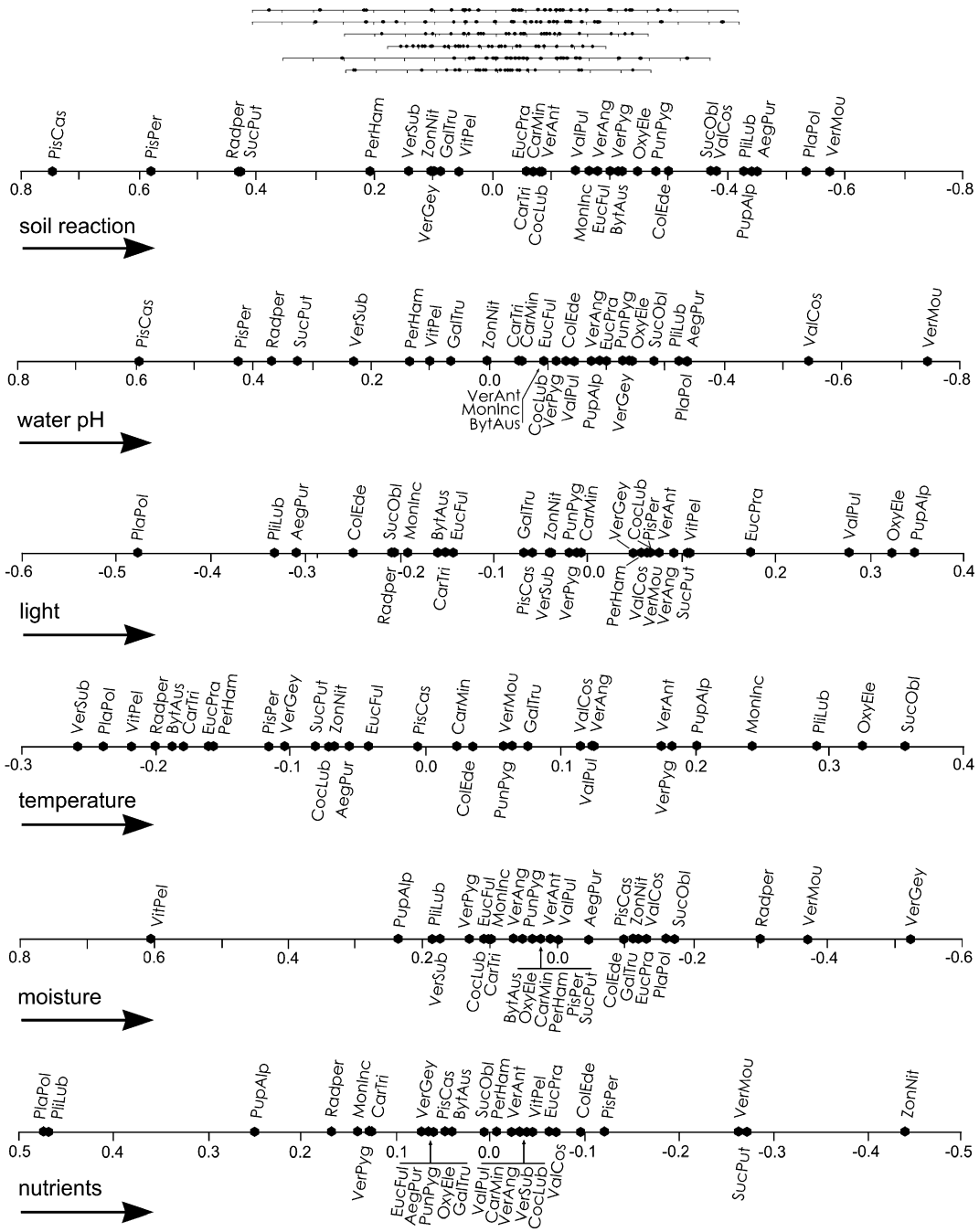


Fig. 4 – Optima of individual species along separate environmental variable gradients. The position means the score on the first partial CCA axis. For each variable the others were used as co-variables including geographical position. The only exception was water pH where the soil reaction was excluded from the set of co-variables and vice versa. For the full species name see Table 1.

this endangered snail was strongly positively correlated with the local water table. In our study this snail's optimum was placed coincidently among the most hydrophilous species (Fig. 4). Another proof of validity of the obtained results is given by typical woodland snails (*Platyla polita*, *Aegopinella pura*, and *Monachoides incarnatus*) and snails commonly occurring in forest habitats (e.g. *Columella edentula* and *Plicuteria lubomirskii*). These land snails, however, are often found in treeless calcium-rich fens, and are considered typical inhabitants of forest ecosystems (Ložek, 1956; Kerney et al., 1983). In concordance with their known habitat preferences, and based on the plant IVs, these snails occurred preferentially in the most shady conditions (see Fig. 4).

The use of plant IVs yields much new knowledge about individual species autecology in fen habitats (Figs. 3 and 4). While detailed analyses of particular species' requirements could not be presented here, we note that many also occur in other, very different, habitats, and may present different

Table 6 – The results of species response curve modelling for six explanatory variables (soil reaction, light, temperature, moisture, continentality, and nutrients)

	Ellenberg scale					
	Soil reaction	Light	Temperature	Moisture	Continentality	Nutrients
Bythinella austriaca s.lat.	–	–	–	–	–	–
Platyla polita	–	–	–	–	–	–
Galba truncatula	–	–	–	–	–	Uni(–)
Radix peregra	–	–	–	Mon(+)	–	–
Anisus leucostoma	Uni(0)	–	–	Uni(+)	Uni(+)	–
Carychium minimum	Uni(+)	–	–	–	–	–
Carychium tridentatum	–	–	–	–	Mon(+)	–
Cochlicopa lubrica	Uni(0)	–	–	–	–	–
Pupilla alpicola	Mon(+)	Mon(+)	Mon(+)	–	–	Uni(–)
Vallonia costata	–	–	Uni(+)	Uni(–)	–	Uni(+)
Vallonia pulchella	Mon(+)	Mon(+)	Mon(+)	–	–	–
Columella edentula	Mon(+)	–	–	–	–	–
Vertigo angustior	Uni(+)	–	–	–	Mon(+)	Uni(0)
Vertigo antivertigo	Uni(+)	–	Uni(+)	–	Mon(–)	Uni(+)
Vertigo geyeri	Uni(0)	Mon(+)	Uni(–)	Mon(+)	–	Mon(–)
Vertigo pygmaea	Uni(+)	–	Uni(+)	Uni(–)	Mon(–)	–
Vertigo moulinsiana	Uni(+)	–	Uni(+)	–	Mon(–)	Uni(+)
Vertigo substriata	–	–	–	–	–	–
Succinella oblonga	Uni(+)	Mon(–)	Uni(+)	Uni(0)	–	–
Succinea putris	Uni(0)	–	–	–	–	–
Oxyloma elegans	Mon(+)	Mon(+)	–	–	–	–
Punctum pygmaeum	Uni(+)	–	–	Uni(0)	–	–
Zonitoides nitidus	–	Mon(–)	–	–	–	Mon(+)
Euconulus praticola	–	Mon(+)	Uni(–)	Mon(+)	–	Mon(–)
Euconulus fulvus	Uni(+)	Mon(–)	–	Mon(–)	–	Mon(+)
Aegopinella pura	–	–	–	–	–	–
Perpolita hammonis	–	–	Uni(–)	–	–	Uni(–)
Plicuteria lubomirskii	Uni(+)	Uni(–)	Uni(+)	Uni(0)	–	–
Perforatella bidentata	–	–	–	Mon(+)	–	–
Monachoides incarnatus	Mon(+)	–	–	–	–	Uni(0)
Pisidium casertanum	Mon(–)	–	–	–	–	–
Pisidium personatum	Uni(–)	Uni(–)	Uni(0)	Mon(–)	–	Mon(+)

Only response curves significant at the P-level of 0.05 are given. For abbreviation of species response curve types see Fig. 2.

spectra of responses to environmental variables in each. Our habitats have a rather low variability in some environmental gradients (e.g. moisture; all sites are wet). Where these are greater, their effects could be more significant.

4.4. *Utilization of Ellenberg's plant indicator systems in animal ecology: advantages and constraints*

Although estimates of environmental variables using IVs cannot provide better information than direct measurements there are several advantages of the approach, particularly under specific conditions. Correctly recorded vegetation plots are less influenced by spatial and temporal variability than single field measurements of environmental factors (Jongman et al., 1987). Opravilová and Hájek (2006) have found that species variation in testate amoebae assemblages was better predicted by species composition of the vegetation than by long-term averages of water chemistry variables. On the other hand, while being independent of expensive analytical equipment, monitoring composition requires advanced skills in plant species identification (Ewald, 2003a) or participation of trained plant specialist in the research (for example of such study see Horsák and Hájek, 2003). Nevertheless, especially for hundreds of study sites over a large area, recording extremely fluctuating variables can be technically difficult and too expensive. The usage of plant IVs can solve the problem and it serves as an estimate of difficult-to-measure factors as well. For example, nutrient contents influencing snail assemblages should be determined repeatedly as a sum of concentrations of various nutrient forms in soil, pore water, litter and aboveground biomass. Such an expensive research may be applicable on several model sites, but not on many localities. Moreover, we do not have data on fine-scale factors such as nutrient availability, vegetation productivity, microclimate or light conditions beneath canopy at our disposal. The scarcity of ecological studies dealing with these factors of a large area across multiple habitats and climatic regions is caused, at least in part, by the logistical complexity and large demands on time and cost of such studies.

In this study we obtained new information concerning fen mollusc ecology on the basis of the estimates of environmental variables using the Ellenberg IVs. We analysed species distributions along factors whose variables are practically impossible to obtain by direct measurements at large scales. In spite of possible biases in estimation, a statistically significant correlation was found between water pH measured in the

field and soil reaction estimated by plant IVs. In addition, autecological knowledge about individual species obtained on the basis of measured water pH and estimated ''soil reaction values'' were almost the same. This feedback is a satisfactory evidence of the plausibility of proposed approach, at least in the case of mollusc ecology in fens.

In principle, plant IVs cannot replace physico-chemical field measurements in animal ecology. However, they can provide valuable information, which can be utilized in animal ecology field studies at both the species and the community levels. As several studies extend Ellenberg IVs to new areas, for example Great Britain (Hill et al., 1999), the Netherlands (Ersten et al., 1998), and Faroe Islands (Lawesson et al., 2003), this plant indicator system can be used over a potentially wider area than only Central Europe.

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